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HEARING IN CETACEANS

EVOLUTION OF THE ACCESSORY AIR SACS AND THE STRUCTURE AND FUNCTION OF THE OUTER AND MIDDLE EAR IN RECENT CETACEANS

14 NOV 1960
PRESENTED

F. C. FRASER and P. E. PURVES

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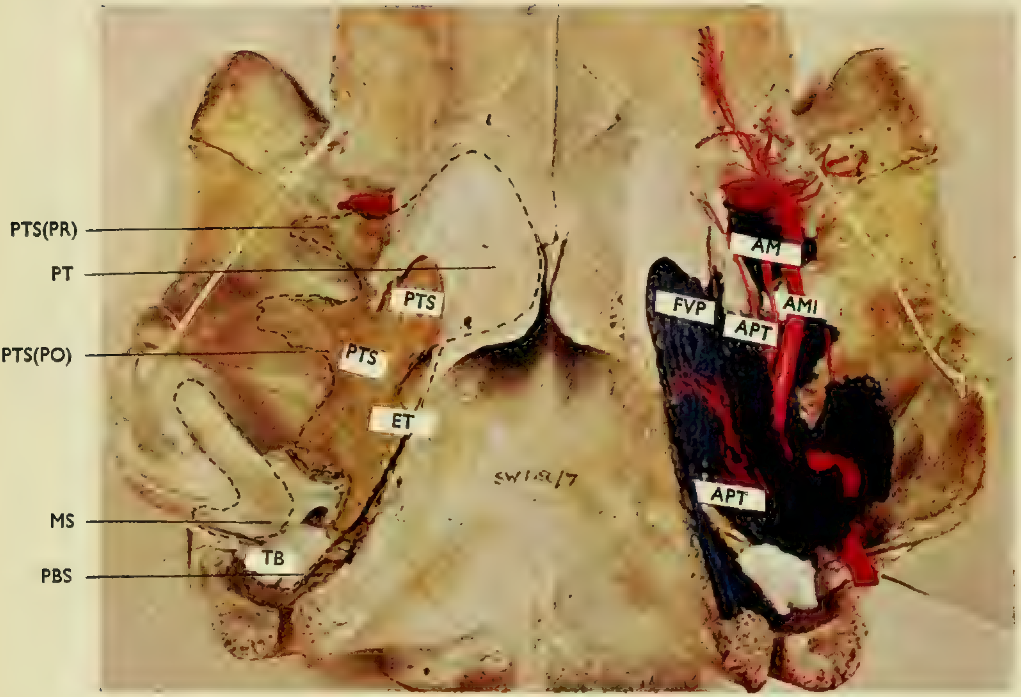

FRONTISPIECE.—SKULL OF A YOUNG PILOT WHALE IN WHICH THE AIR SINUS SYSTEM AND ITS VASCULAR NETWORK HAVE BEEN INJECTED WITH POLYESTER RESIN.

AM —Mandibular artery.
AMI—Internal maxillary artery.
APT—Pterygoid artery and arterial branches to internal pterygoid muscle
ET —Eustachian tube.
FVP—Fibro-venous plexus.
MS —Middle sinus.

PBS —Peribullary sinus.
PT —Pterygoid bone.
PTS —Pterygoid sinus.
PTS (PR)—Preorbital lobe of pterygoid sinus.
PTS (PO)—Postorbital lobe of pterygoid sinus
TB —Tympanic bulla.

By Courtesy of "ENDEAVOUR".

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HEARING IN CETACEANS

EVOLUTION OF THE ACCESSORY AIR SACS AND THE STRUCTURE AND FUNCTION OF THE OUTER AND MIDDLE EAR IN RECENT CETACEANS

By F. C. FRASER AND P. E. PURVES

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Notes. In the diagrams referred to in Figs. 16–21 as "transverse section" the plane of the section is through the foramen ovale and pterygoid hamulus. Owing to the progressive displacement forward of the hamuli from the foramen a varying degree of obliquity is introduced.

In relating Diagrams 22–25 to the skulls figured in Plates 5–47, it should be remembered that the latter represent ventro-lateral views of the skull.

Contractions used in the text-figures are to be found in the Key, Page 137.

HISTORY

In their previous paper (Fraser and Purves 1954) the writers made reference to the subject of pressure equalization and adjustment on either side of the tympanic membrane in the Cetacea. It was shown that Beauregard was the first to suggest a hypothesis which appeared to satisfy all the anatomical and physical requirements of the conditions encountered by cetaceans in their natural environment. Beauregard was however by no means the first to recognize the existence of the accessory air sinuses of the middle ear, and as a preliminary to the writers' own observations a brief historical summary of the earlier work on this subject is required.

Camper (1777) gives reference to Joh. Dan Major as the discoverer of the peribullary sinus in the year 1672, quoting the latter's paper he states " one should know that the petrous bones are not tightly attached to the cranium, but are lying loosely between the flesh and the fat close to the base of the brain and the occiput, at the side of the head, in a sinus, which is formed by two processes which do not touch each other ". Dan Major thus antedates Tyson (1680) who in his *Anatomy of the Porpoise* made much the same observation.

Hunter's (1787) description is a little more detailed. It is as follows :

" The Eustachian tube opens on the outside of the upper part of the fauces ; in some higher in the nose than in others ; highest I believe, in the Porpoise. From the cavity of the tympanum, where it is largest, it passes forwards and inwards, and near its termination is very much sacculated, as if glandular ".

" The Eustachian tube and tympanum communicate with several sinuses, which passing in various directions surround the bone of the ear. Some of these are cellular, similar to the cells of the mastoid process in the human subject, although not bony. There is a portion of this cellular structure of a particular kind, being white, ligamentous, and each part rather rounded than having flat sides. One of the sinuses passing out of the tympanum close to the membrana tympani goes a little in the same direction and communicates with a number of cells ".

" The whole function of the Eustachian tube is perhaps not known ; but it is evidently a duct from the cavity of the ear, or a passage for the mucus of these parts ; the external opening, having a particular form would incline us to believe that something is conveyed to the tympanum ".

Monro (1785) from the results of the dissection of a porpoise appears to have been the only writer to suggest the relationship of the air sinuses with the frontal, sphenoidal and maxillary sinuses of terrestrial mammals and it is noteworthy that these sinuses as such are totally absent in cetaceans.

Home (1812) found in *Balaena mysticetus* that the Eustachian tube had a similar glandular and sacculated appearance to that seen by Hunter in the porpoise.

Rapp (1837) made a review of the existing information about the cetacean ear and demonstrated in the porpoise the relation of the air sacs to adjacent bones. He stated that the anterior end of the tympanum was open and extended into a branching sinus. In front of the cavity of the tympanum lay a membranous, ovoid cavity over an inch long and wide enough for the insertion of a finger. Its upper and inner wall lay immediately against the bony surface of the skull. Branches extended further out, one forward, ending in the cavity of the pterygoid bone. Another went somewhat higher and forward to the outer side of the ascending branch of the palatine, and ended blindly, immediately behind the tooth row of the upper jaw. Still another branch went upwards, and passed into a bony canal which was found in the bone of the upper jaw, ascending on the outer side of the nasal cavity, until it reached the frontal bone and ended blindly. An extension of the main sinus passed outwards and ended under the supra-orbital process of the frontal, and finally a backward extension passed between the ear bones and the ridge of the basioccipital bone. All the sinuses were lined by a thin, and on the inner surface, smooth, white, glandular membrane. He described the Eustachian tube and in addition to what was already known, noted the absence of cartilage in its structure and that it passed through no bone. He observed the presence of crescent-shaped valves projecting into the lumen of the tube and directed towards the nares. In his opinion the valves could not quite close the lumen. Rapp gave a description of the pterygoid muscles and in general Stannius' (1849) account agrees with that of the former author.

Carte and Macalister (1868) gave an account of the dissection of a Lesser Rorqual which, in addition to a short description of the osteology and musculature of the pterygoid region, included a more detailed reference to a very remarkable plexus of arteries and veins which lay in a distinct cavity bounded internally by the pterygoid muscle and externally by the angle of the mandible and fibro-cartilage. The cavity was lined by an extremely delicate, glistening, membranous structure, similar in texture and appearance to the serous lining membrane of the veins. The vascular plexus itself extended from the coronoid process of the lower jaw to a point midway between the angle of the latter bone and the upper border of the sternum. The venous ramifications that partly formed the plexus gradually united as they passed backwards and ultimately formed one trunk, the jugular vein.

In the course of his work on the anatomy of the Pilot Whale (*Globicephala melaena*) Murie (1878) noted several anatomical features which he considered to be common to cetaceans in general. " In all the Cetacea cut up by me I have observed well developed and separate *pterygoidei*. The external, flat, broad, fleshy and of a quadrilateral shape, is fixed to the outer surface of the pterygoid plate and with a downward and forward plane goes to the inner surface of the lower jaw chiefly to the upper margin of the bone. The internal muscle arises from the superficies of the prominent portion of the pterygo-palatine, passes backwards and downwards to the mandible. Inferiorly and on its posterior border, the latter muscle sends off tendinous fibres which join those of the articulating condylar process of the mandibular." Following a description of the tympanic bulla and neighbouring tissues which coincides with those of earlier writers he goes on, " The Eustachian canal as it leaves the tympanic bulla, has considerable diameter and retains it more or less uniform as it passes towards the fauces. A tough membrane and retia mirabilia lie superficial to it ".

Later he states : " Of the cranial vascular distribution, circumstances did not permit me to master it in detail. The more notable observations I could make were chiefly regarding a great plexus situated at the inferior base of the skull and situated with a rete occupying the proximal infundibular cavity of the mandible. I subsequently had an opportunity of investigating the same in *Grampus* and *Lagenorhynchus* where it likewise obtains ".

" The internal maxillary artery having passed deeply behind the lower jaw, and made a bend, sends forwards a long inferior dental artery. As this pursues its course it distributes ramifications among the fatty matters and plexus presently to be mentioned. The mandibular cavity contains a mass of softish, marrow-like substances held together by a network of fibrous tissue. Moreover the interstices are occupied with a maze of vascular channels partly composed of arterial and partly of venous capillaries interwoven irregularly. Next the bone the tissue and vessels are firmly adherent to the periosteum in some cetaceans, e.g. the great *Balaena mysticetus* and *Balaenoptera musculus*, as I myself have been a witness to, the cavity in question possesses a perfectly enormous amount of oily material. Even in smaller genera the quantity is by no means sparse ; so that the tissues hereabouts as a whole and on section may be compared to blubber supercharged with blood vessels. Further on, the internal maxillary gives off large muscular branches and others forming pterygo-maxillary divisions. These latter were not followed into the cranium. The inferior base of the skull, from the tympanic bone forwards to the maxillary, internally bounded by the levator and sphincter muscles of the posterior nares, represents one continuous rete mirabile. This spongy network of vessels lies upon a thick layer of fibroid tissue, and the vessels anastomose with the aforesaid mandibular rete whilst they likewise appear to inter-communicate with another venous locular network behind and at the root of the Eustachian tube. The venous capillaries collect into a jugular channel more or less connected with the rete of the neck ".

Anderson (1879) in his account of the anatomy of *Platanista* found the situation of the air sacs so comparable with the " guttural pouches " of the Perissodactyla that he refers to them as such.

His description reflects the highly involved and complicated arrangement of these cavities but essentially they are a paired structure each member of which originates from the Eustachian tube. Part of each sac lies between the stylo-hyoid and the thyro-hyal, forming attachments to these, with its internal wall against the the outer wall of the back of the pharynx while the roof of the sac lies below the exoccipital and basioccipital bones. The inner surface of the sac is " white, smooth, glistening and tendinous in appearance and its wall has numerous deep recesses of various dimensions formed by arching folds of the membrane constituting the walls of the sacs—some of the recesses lead into small secondary pouches and from from these into a labyrinth of smaller passages."

" A pair of diverticula from these sacs converge in front of the thyroid cartilage where they are separated only by a thin membrane ".

Of the microscopical appearance of the Eustachian sacs Anderson says that they are composed of loose folds of thick mucous membrane. " Flat, irregular papillae invest the surface, and everywhere, . . . are small pits and minute orifices of mucous glands. These glands are most of them superficially situated but some are sunk deeper into the tissue, chiefly simple and tubular. Certain of them nevertheless are slightly racemose ; and all contain cylindrical epithelium with often a central cavity. The elevated papillae are exceedingly vascular, indeed possess a thick network of fine capillaries the parent vessels of which are both numerous and of considerable calibre. The free surfaces of the papillae are covered by a close-set layer of cylindrical, fringed or ciliated epithelium. The deep connective tissue of the submucous membrane is loose, strong fibred, but very open, some fat cells and oily particles being mingled with the tissue, while elliptical-shaped great bundles of striped muscular fibres course in different directions, right up almost to the glandular layer in some instances ".

The contributions of Beauregard (1894) to the knowledge of the anatomy and physiology of the organ of hearing of mammals constitute a major advance, especially to the extent that they concern cetaceans. He was the first person to inject the sacs of the middle ear and to give names to the component parts. In addition he puts forward a physiological hypothesis of their function which appears to be more acceptable than those of earlier writers. Having successfully injected the middle ear and sacs, both of Odontoceti and of Mysticeti, the following features were noticed. In the Common Dolphin the Eustachian tube was funnel-shaped anteriorly, its orifice a longitudinal slit in the posterior region of the nares. The tube was about 4 mm in diameter and lay against the bony wall of that part of the nostril formed by the pterygoid. For two centimetres from its orifice the tube passed obliquely outwards and posteriorly along a notch formed by the sphenoid and pterygoid. The mucous membrane of the tube was areolar throughout its length. There was in addition on the inner wall, a longitudinal fibrous ridge which extended to the lower wall of the tube and united with it near the entrance to the bulla. The duct was thus divided into two parts, one external, which terminated in a cul-de-sac, and another internal, which showed inside an orifice, joining the end of the bulla and making communication between the Eustachian tube and a vast air cavity emanating from the bulla. The orifice in question measured one cm long by three mm wide and was placed in such a way that by its intermediate position it communicated simultaneously with the blind canal, the tympanic cavity and air sacs.

A downward extension of the squamosal, a characteristic feature of all cetaceans, was designated the *falciform process*, a name by which it is now recognized. The names employed by Beauregard for the divisions of the sinus system are so generally applicable that they will be used as applied by Beauregard throughout this paper with one exception. The following is a summary of Beauregard's description. The sacs or sinuses are as follows :

1. *The Anterior Sac.*
2. *Pterygoid Sac.*
3. *Peribullary Sac.*
4. *Posterior Sac.*
5. *Medial Sac.*

All of these cavities communicate with the middle ear proper.

The anterior sac. This is very large—extending over all the ventral surface of the cranium anterior to the falciform process, surrounding the foramina of the cranial nerves and penetrating between the irregularities of the bone in the frontal and preorbital regions. In the Common Dolphin it is prolonged in a deep channel extending in the ventral surface of the maxilla for about two thirds of the latter's length. (As the greater part of the sac has been identified by the present writers as belonging properly to the pterygoid sac, the use of " Anterior Sac " will be restricted to that part of the system projecting beyond the posterior limit of the rostrum).

The pterygoid sac. A large diverticulum, filling the deep cavity which the palatine and pterygoid make as they fold below the sphenoid, is given the name of the pterygoid sac. Part of the Eustachian tube in its course to its external opening lies in close apposition to this sac.

The peribullary sac. Beauregard's anterior sac communicates posteriorly with a space which lies between the periotic and the bones of the cranium. This cavity, limited mesially by the occipital crest and dorsally by the dura mater contains the ear bones. The fibrous, saccular extension from the " anterior sac " which lines the cavity is called the peribullary sac. Beauregard pointed out that it does not extend to the ventral surface of the bulla which is covered in this region by a thick pad of fibrous tissue.

The posterior sac. The posterior sac communicates with the tympanic cavity by the posterior orifice of the bulla. It occupies the concavity of the paroccipital process. This cavity is sheathed in thick cartilage and enveloped anteriorly and posteriorly in a strong cushion of fat.

The medial sac. The medial sac communicates with the tympanic cavity by the petro-tympanic orifice and is situated under the concave surface of the zygomatic process, internal and posterior to the glenoid fossa. It is prolonged into the groove formed in this region and is limited anteriorly by the curved and concave border of the falciform process. The present writers will refer to the concavity in the squamosal in which the medial sac is lodged as the tympano-squamosal recess.

All the sacs are distinguished by the presence of numerous trabeculae which divide their cavities into complicated air pockets. Blood vessels, especially veins, form a rete of great richness. From the superior wall of the great "anterior sac" a thick, prominent ridge of mucous membrane protrudes, which is areolar and very vascular and gains access to the bulla by which it penetrates the tympanic cavity. This fold, reduced to very nearly a cylindrical cord when it enters the cavity, is there developed into a spongy mass which passes along the whole length of the bulla. Beauregard goes on to say that it is attached by its concave border to the anterior process of the external lip of the bulla, then to the body of the malleus near the tubercle to which is attached the ligament of the tympanic membrane. It terminates by an enlarged extremity near the fenestra rotunda, fixing itself to the base of the mastoid process.

According to Beauregard, the relationship of this spongy mass with the hammer and the anterior orifice of the bulla gives rise to the supposition that it acts as a muscle for the malleus ; but on microscopic examination he was unable to find any trace of muscle fibres. (For discussion of this see page 29).

He injected the vessels of the region of the ear of a foetal dolphin 110 cm long. He found that the internal carotid artery accompanied by the (internal) jugular vein passed along the deep notch separating the basi-occipital from the mastoid region. It penetrated the tympanic cavity in the space which limits the internal lip of the bulla and the groove which separates the posterior promontory of the bulla from the periotic. In this first part of its course the internal carotid artery was a neighbour of the facial nerve. In the tympanic cavity it occupied the long axis of the spongy mass and measured not less than 3 mm in diameter. Its course was sinuous. It made a curve towards the dorsal convexity, another towards the ventral convexity, and then made straight towards the anterior extremity of the tympanic cavity. It emerged from that extremity and penetrated the great " anterior air sac ", crossing the latter obliquely before entering the carotid orifice of the cranium. During its passage across the tympanic cavity the carotid artery was found to be enveloped in a voluminous venous plexus, the varicose ramifications of which measured from 1–5 mm in diameter. This plexus, mixed with fibrous tissue is the enigmatic spongy organ. Beauregard considered the spongy organ, in common with all the other venous retia in the pterygoid region, to be erectile, but this aspect of his hypothesis will be discussed later (pages 119–120).

Beauregard continued his researches by injecting the air sinuses of a Lesser Rorqual. He found that the Eustachian tube, in its course rearwards, passed between the angle formed by the inferior border of the sphenoid and the hamular process of the pterygoid. Subsequently it connected with a large ovoid sinus occupying the pterygoid. He considered the sinus to be an enlargement of the posterior extremity of the Eustachian tube, and established the connection between these and the tympanic cavity proper. He homologized a large cavity on the upper and mesial surface of the bulla with the peribullary sac, and similarly a small diverticulum at the posterior extremity of the bulla was recognized as the posterior sac.

Finally Beauregard identified the "glove finger" of the tympanic membrane with the medial sac, but the present writers (Fraser and Purves, 1954) suggested its relationship with the "pars flaccida" (but see also p. 113–5).

Denker (1902) examined the ear region of cetaceans and although not dealing with the anatomy of the air sinuses suggested a possible means by which they function.

The work of Boenninghaus on *Phocaena phocoena* contained in two monographs produced in 1902 and 1904 constitutes the most comprehensive study of the anatomy of the throat and ear of cetaceans ever published. The earlier paper is concerned chiefly with the musculature of the throat and nose, and the other more particularly with the ear. Parts of the latter paper are more relevant to the subject of the air sinuses but it is necessary in the survey of them which follows to include extracts from the earlier work. His long, detailed description of the bones of the base of the skull recapitulates what has been written by a number of earlier writers and need not be repeated. Information about the morphology and relationships of bones concerned with the air sacs can be seen on Pls. 5–47. As the musculature and associated structures of the throat and mouth are important in the comprehension of the evolution and function of the air sacs, a more detailed note must be made of Boenninghaus' findings. These will be dealt with in the following order: (1) Musculature of the posterior nares; (2) the soft parts of the pterygoid region in general; (3) the fibrous supporting tissue of the skull base; (4) the intra-mandibular fatty body; (5) the pterygoid and palatine muscles; (6) the arteries; (7) the veins.

1. *Musculature of the posterior nares.* According to Boenninghaus, the muscular complex of the posterior nares is made up of the following elements: (*a*) m. constrictor-pharyngeus-superioris, (*b*) m. palato-pharyngeus, (*c*) m. thyro-palatinus, (*d*) m. salpingo-pharyngeus, (*e*) m. levator palati, (*f*) m. tensor palati, (*g*) m. stylo-pharyngeus.

(a) *Constrictor-pharyngeus-superioris.* "The whole pars superioris of the pharynx has been greatly drawn out by the up-turning and lengthening of the presphenoid, thereby the form of the rear wall has become changed. In land mammals the m. constrictor inferioris seen from behind partly covers the m. constrictor medius and the latter partly covers the constrictor superioris. The constrictors lie like the slides of a half-open telescope, one over the other. In *Phocaena*, however, the m. constrictor superioris is completely withdrawn from the medius and inferioris. The gap thus created is filled by the palato-pharyngeus ".

(b) *M. palato-pharyngeus.* " The inner face of the muscular pharynx of *Phocaena* is formed, except at the palato-pharyngeal arc, by a single, extended, thick muscle, the fibres of which lie parallel, while they are in the posterior nares, then behind these radiate fan-wise in sweeping lines towards the rear of the pharynx so that the lowest fibre layers encircle the epiglottis. At their posterior extremity the fibres merge bilaterally but do not form a raphe. This muscle is further distinguished by the fact that near its lower end a powerful sphincter muscle 9 cm thick arises from its inner surface and is so formed that its superior surface merges without boundary into the m. palato-pharyngeus. Its ventral, sharper rim lies mesial to the latter and forms the mesial boundary of a pair of lateral pockets open dorsally. This sphincter lies underneath the swelling of the mucous membrane known as the arcus pharyngeus which tightly encloses the upper part of the epiglottis and arytenoid cartilage."

(*c*) *M. thyro-palatinus.* " From the ventral rim of this constrictor some bundles (of muscle fibre) emerge which do not encircle the epiglottis but proceed laterally and ventrally to be inserted into the thyroid cartilage. This extension of the pars interna of the m. palato-pharyngeus is known otherwise only in man and the horse and is named the thyro-palatinus."

(d) *M. salpingo-pharyngeus.* " From the ventral extremity of the bony nares a muscle originates, which, like the constrictor superioris passes obliquely and medially downwards. Having emerged from the nares it lies alongside its counterpart from the other nostril for a short distance and eventually merges with its fellow. Only a narrow streak of the m. salpingo-pharyngeus can be observed from the inner aspect of the naso-pharynx but on the outer aspect of the naso-pharyngeal muscle mass it can be seen to widen considerably and overlie the united superior constrictor palato-pharyngeus (pars externa). At its ventral extremity the m. salpingo-pharyngeus unites, by means of a light inscriptio tendinea . . . with the m. longitudinalis oesophagi."

(e) *M. levator palati.* " From the upper border of the naso-pharynx there arises a muscle which encircles the boundary of the pterygo-palatine attachment of naso-pharyngeal muscle mass from front to rear in a pointed curve. At the anterior narial wall it dips downward, lying close to the septum and finally merges without visible boundary into its respective half of the pars interna of the palato-pharyngeus."

" In its string-like outer form, as in the delicacy and lighter colouring of its fibres it corresponds so completely with the pars interna of the m. palato-pharyngeus and its continuation, the arcus palatinus that the whole gives the impression of forming a combined muscle system."

(f) *M. tensor palati.* " At the lower margin of the posterior nares and attaching to the origin of the m. salpingo-pharyngeus some delicate muscle streaks leave the region of the mouth of the Eustachian tube and radiate between the fibres of the m. constrictor superior obliquely without our being able to follow them between these fibres for any considerable distance." Boenninghaus reports that Zuckerhandl confused the tensor palati with the internal pterygoid saying "certainly the tensor palati is to be found in this position in all other mammals except in the whales, i.e. between the internal pterygoid and the Eustachian tube". This is discussed in the present paper on p. 19.

(g) *M. stylo-pharyngeus.* "This is originally an unpaired muscle which springs from the floor of the posterior nares and diverges into two limbs each of which is attached to the rear part of its respective styloid. The free outer face of the muscle is streaked longitudinally and without a raphe, on the inner face the fibres lack any definite direction and are firmly fused with the ventral face of the m. palato-pharyngeus."

2. *The soft parts of the pterygoid region.* Boenninghaus dissected the pterygoid region in three stages, shown in Pl. 1, figs. *a*, *b*, and *c* (corresponding to his Pl. 12, figs. 3, 4 and 5). The first, the most superficial stage, shows the following structures (fig. *a*). The bony nasopharynx is filled by the naso-pharyngeal muscle mass which rises into the nose through the "false choanae" (Pl. 1, fig. *a*). The whole lateral part of the skull base is covered by the m. pterygoideus internus (2) under which posteriorly can be seen the eminence of the tympanic bulla (17). The m. pterygoideus internus and the pharynx are separated by the pterygoid ligament (5′). When the attachment of the pterygoid muscle is separated from this ligament, and the muscle reflected, one sees that the ligament forms the ventral edge of a mass of tissue, smooth and membranous posteriorly, and anteriorly pierced by large holes. The holes give entry to the vena pterygoidea (16) and to the pterygoid fibro-cavernous venous plexus. Laterally the m. mylo-hyoideus is reflected over the jaw. Boenninghaus' next figure (Pl. 1, fig. *b*) depicts a dissection made one cm more dorsally than that of fig. *a* and from which the naso-pharyngeal muscle mass has been removed. As seen in the figure, the following structures are to be distinguished. Laterally from the pterygoid (18) the Eustachian tube is open at its distal end and leads into the vestibulum pneumaticum (8), this in turn leads into the bulla (17) in which is a conspicuous body (17′) the corpus cavernosum tympanicum. Beside the tube one sees the pterygoid fibro-cavernous venous plexus (5′). The massive fatty body of the lower jaw (6), as well as the jaw itself, can be seen. The third dissection (fig. *c*) is again one cm deeper than the previous one. The pterygoid bone, the lower jaw, fatty body and the pterygoid muscle have been removed. The anterior pneumatic cavities (9, 10, 11) are seen to be connected with the vestibulum pneumaticum (8). Overlying this is the pterygoid fibro-cavernous venous plexus (5′).

In the figure there are probes from space to space.

3. *The fibrous supporting tissue at the skull base.* The skull base of the toothed whales has a supporting tissue which is not found in any land mammals. From this, continues Boenninghaus, it may be assumed that it plays some important role in these aquatic mammals One can distinguish posteriorly a smooth, flatter, non-perforate part from an anterior portion which is thicker and pierced by many veins. The rear part covers the bulla while the anterior part lies in front of it. The fossa of the skull base which contains the tympano-periotic bones is closed ventrally by a fibrous membrane which covers the ventral surface of the tympanic bulla, and is attached to the cartilaginous ventral edges of the basi-occipital, the paroccipital

and the zygomatic process of the squamosal. This tissue bridges the paroccipital fissure and is penetrated by the meatus and facial nerve. Boenninghaus makes the important indication that he regarded the tissue as the perichondrium or the periosteum of the bones just referred to. The tissue round the bulla is up to 1 cm thick and is strongly attached to the roughened, ventral surface of the latter, acting as a support ventrally for the bulla.

From the posteriorly directed tip of the ala palatina (19) and from the adjacent plate of the pterygoid (8) there originates a wide, reticular, ventral membrane. It is directed posteriorly towards the supporting tissue of the bulla and merges with it. Mesially it covers the Eustachian tube (7, fig. *b*) and the vestibulum pneumaticum (8) and ends ventrally in a ligament-like edge, the pterygoid ligament (5″, fig. *a*). Laterally the membrane has a wide attachment to the falciform process. Part of the membrane in this region does not fasten on to the wide line of attachment but runs more posteriorly and laterally, surrounding the bulla, and merging with the thickened periosteum of the zygomatic process. This membranous tissue is traversed by many large and small intercommunicating, venous cavities which appear oval in transverse section. It has extensions which pass round the median aspect of the Eustachian tube and through the gaps in the skull to the dura mater. There is also an extension from the zygomatic process of the squamosal to the post-orbital process of the frontal (fig. *22c*,) which closes the otherwise incomplete orbit ventrally.

4. *The intra-mandibular fatty body*. On the inner surface of the lower jaw of toothed whales is a fatty body of considerable size (Pl. 1, fig. *b*). An interesting peculiarity of the lower jaw is that the posterior half of the median wall is completely absent. The anterior half ends in a posteriorly open arcuate edge which forms the entrance to the wide mandibular hiatus corresponding to the mandibular foramen of other mammals. The wide, bony trough at the hinder end of the lower jaw is occupied by the fatty body. Boenninghaus considers this to be the bone marrow of the posterior half of the lower jaw, and states that it is covered by a strong fibrous tissue continuous with the periosteum of lateral aspect of the lower jaw, and forms an attachment for the pterygoid and mylo-hyoid muscles (see fig. *b*). The fatty body is traversed by the mandibular vessels and nerves and a strong fibrous tissue with a wide mesh. The marrow lying in this tissue mesh is not of the usual consistency but is semi-liquid and oil-like. It has a tendency to hypertrophy since it sends out extensions covered by periosteum in various directions. It forces its way to the mylo-hyoid (Pl. 1, fig. *b*, 5) and grows forward over the edge of the hiatus mandibularis for some distance, lifting the pterygoid muscles from the ventral border of the jaw. Also a further extension lies in the deep trough adjacent to the ventro-lateral aspect of the bulla and, according to Boenninghaus, is continuous with the supporting fibrous tissue of the latter.

5. *The pterygoid muscles*. According to Boenninghaus the internal pterygoid muscle (2 in Pl. 1, figs. *a* and *b*) covers the whole of the ventro-lateral skull base. It originates from the lateral edge of the maxilla, from the lateral edge of the palatine, from the palatine process of the pterygoid, from the pterygoid ligament and from the basioccipital process. From these attachments the fibres stretch obliquely backwards and outwards and are inserted into the mesial periosteal wall of the lower

jaw fatty body. Posteriorly it is attached to the fibrous sheath of the bulla and anteriorly to the bony part of the mandible (but see p. 18).

The external pterygoid lies dorsally and laterally to the internal pterygoid and has a similar but more dorsally situated origin. Its insertion is also partly on the periosteum of the marrow and on the narrow dorsal edge of the posterior portion of the lower jaw. Its course is obliquely outwards and more horizontal than that of the internal pterygoid (but see p. 17–18).

6. *Arterial supply.* Boenninghaus describes the vascular system of the base of the cranium in great detail, but only certain features of his account are relevant to the present paper. His main concern is with the course and atrophy of the internal carotid artery and with the alternative cranial blood supply through the spinal meningeal arteries. Nevertheless, the diagram which he uses to illustrate the first of these features is useful for showing the external carotid and its extensions, although Boenninghaus regarded it as unnecessary of mention in his text. The figure (Text-fig. 1) shows the very short innominate artery giving rise soon to the internal and external carotids. The external carotid curves slightly round the lateral aspect of the tympanic bulla after having given off a branch labelled " external maxillary " by Boenninghaus but more correctly to be interpreted as the transverse cervical, it passes forward lateral to the air sacs and gives off a plexus of vessels supplying the fibro-cavernous venous plexus ; at about the same point the temporal artery originates. The main stem continues anteriorly as the internal maxillary.

7. *Venous drainage.* As with arterial supply so with the venous drainage system Boenninghaus' account is very involved and difficult to follow. It is perhaps best understood, for the purpose of later discussion (p. 29) by reference to his schematic diagrams (Text-fig. 2) reproduced here. Although his identification of the main venous trunks, coincides with that of the present writers his interpretation of some of the details is open to criticism.

Hanke (1914) examined the foetuses of several whalebone whales and was able only to identify the peribullary and medial sinuses. " The largest of the pneumatic cavities the sinus pterygoideus seems to develop at rather a later stage and its size and position is influenced by the position of the tympano-periotic." He further noted that while in the embryo the pterygoid is in contact with the anterior margin of the bulla, in the adult there is a gap of as much as 10 cm between the two.

Brazier Howell (1930) observes that " in the whalebone whales (at least in *Balaenoptera*) the anterior part of the bulla projects into a fossa the size of one's two fists and in freshly killed specimens this is entirely filled with a coarse foam of albuminous rather than greasy texture. . . . There is free communication between this fossa and the choanae. In the odontocetes there is a different but analogous system of air sinuses adjoining the middle ear, and connecting with an intricate labyrinth of ducts. Authors have been very vague and cautious about describing these ducts, and with good reason, for without the injection of a suitable coloured mass into this part of the freshly killed specimen their proper definition is utterly impossible as their finer ramifications are otherwise not to be distinguished from adjoining blood vessels and oil ducts. It must therefore suffice to say that this system of air sinuses communicates with the choanae and apparently sends trabeculated branches rami-

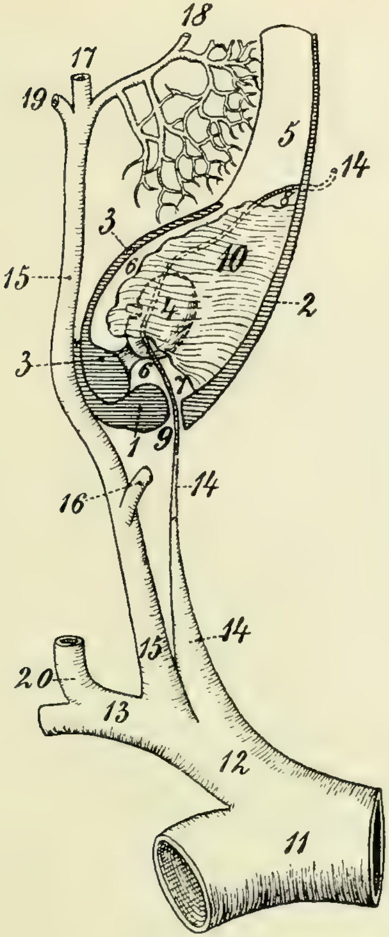

FIG. 1. Boenninghaus' (1903) figure of the course of the internal carotid artery, right side ventral view, of *Phocaena*, 116 cm. long.

1. Paroccipital process. 2. Basioccipital. 3. Tympanic bulla. 4. Periotic. 5. Eustachian tube (= Boenninghaus' vestibulum pneumaticum). 6. Tympanic cavity. 7. Posterior aperture of the tympanic cavity. 8. Anterior entrance of the same. 9. Paroccipital notch. 10. Corpus cavernosum. 11. Aortic arch. 12. Innominate artery. 13. Subclavian artery. 14. Internal carotid artery. 15. External carotid artery. 16. External maxillary artery. 17. Internal maxillary artery. 18. Pterygopalatine artery (or plexus). 19. Deep temporal artery. 20. Occipital artery.

fying through the peculiar fatty tissue that occurs in odontocetes within the angle of the lower jaw."

Anthony & Coupin (1930) appear to be the first to have described the air sacs of a ziphioid, *Mesoplodon bidens.* The extent of their observations is limited by lack of material. Comparison is made between the guttural pouch of various Perissodactyls and the Beaked Whales' air sacs. " In *Mesoplodon* the gutteral pouch consists of a large bag of which the two expansions, one superior and posterior (the smaller), and the other inferior and anterior, are lodged on the external face of the pterygoid bone."

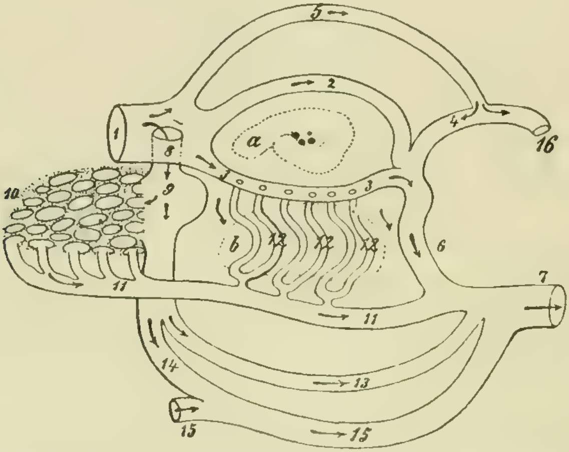

FIG. 2. Boenninghaus' (1903) figure of the venous drainage of the base of the cranium in *Phocaena.*

1. Cavernous sinus. 2. Superior petrosal sinus. 3. Inferior petrosal sinus. 4. Transverse sinus. 5. Longitudinal sinus. 6. Internal jugular vein. 7. Common jugular vein. 8. Emissary vein from the foramen lacerum medium. 9. Bulbous venosus epibularis of Boenninghaus. 10. Fibro-venous plexus of the pterygoid. 11. Pterygoid vein. 12. Corpus cavernosum. 13. Ramus bulbi venosi ad jugularem internam of Boenninghaus. 14. Ramus bulbi venosi ad jugularem externam of Boenninghaus. 15. External jugular vein of Boenninghaus. 16. Spinal venous plexus. *a.* Periotic, *b.* tympanic bulla.

Scholander (1940) in his classic paper on the respiratory function in diving animals and birds states " On the inner rear side of the lower jaw of the Bottlenose on each side, is an air recess, each with a maximal capacity of about 1 l. The recesses are in open connection with the nasal cavity and can be completely collapsed."

Finally Yamada (1953) figures, but does not describe in detail, the arrangement of air sacs in *Berardius bairdi* and *Kogia breviceps.*

The foregoing historical account of the structure of the accessory air sinuses in cetaceans is in general agreement with the writers' own finding, with certain reservations which will be discussed in the following sections.

BASICRANIAL ANATOMY

PTERYGOID AND NASOPHARYNGEAL MUSCLES

(1) DELPHINUS

In his dissections of *Phocaena phocoena* Boenninghaus described a supporting tissue of the skull base which is fully referred to on p. 12. The present writers have found that this tissue is present in all the odontocetes examined by them—*Phocaena phocoena, Lagenorhynchus albirostris, Globicephala melaena, Grampus griseus, Tursiops truncatus* and *Delphinus delphis*. A dissection of the last species is shown in Text-fig. 3. The "wide reticular, ventral membrane (PS) directed posteriorly towards and merging with the supporting tissue of the bulla" is more extensive than Boenninghaus suggests. In fact it constitutes the whole lateral wall of the air sinus system and its histology will be described in the next section. In Pl. 4A it will be seen that voluntary, striped muscle (MFS) is attached to the outermost layer of fibrous tissue (TF). This voluntary muscle is a small part of the pterygoid musculature now to be described.

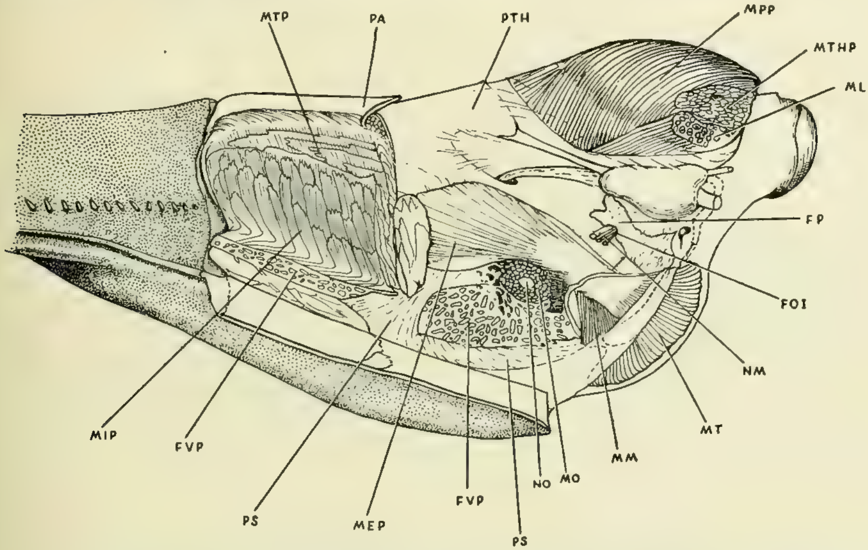

FIG. 3. Dissection of the right half of the head of *Delphinus delphis*, after removal of mandible and posterior part of palatal musculature, to show inter-relationship of muscles and periosteal sheet.

External pterygoid muscle. The external pterygoid muscle (MEP) in *Delphinus delphis* (Text-figs. 3 and 4) is similar in position and extent to that described by Boenninghaus for *Ph. phocoena* but in the former, attachments were observed which were not described by this author. As noted by him there is an attachment to the narrow dorsal edge of the posterior portion of the mandible (MD). In addition there is a more ventral attachment (VTEP) to the fibro-cartilaginous articulation of the lower jaw (MD), which is homologous with the insertion of the pterygoid muscle of man into the articular capsule. On its mesial aspect the muscle is attached at its anterior extremity to the lateral aspect of the tip of the posteriorly directed lateral lamina of the palatine bone, but its greater part on this aspect is attached to the fibrous external wall of the air sinus.

Internal pterygoid muscle. The present writers do not agree with Boenninghaus in his identification of the internal pterygoid muscle (MIP). The ventro-lateral muscle mass identified by him as the internal pterygoid is, in *D. delphis*, clearly divisible into two distinct portions separated by fascia. Only the more anterior portion has the attachments normally associated with the internal pterygoid muscle, namely—as in man—palatine, pterygoid, maxilla, and inner face of lower jaw. This muscle is attached to the ossified palatine bone and to membranous, unossified portions of the air sinus system in the neighbourhood of the other three bone elements. These membranous areas are derived from pterygoid, maxilla and mandible. The position of the internal pterygoid in relation to the external, is such that the qualifications used are misnomers. The internal pterygoid muscle is displaced anteriorly so that it lies entirely in front of, and not alongside, the external pterygoid. In man the internal pterygoid is described as a thick, quadrilateral muscle whereas in the

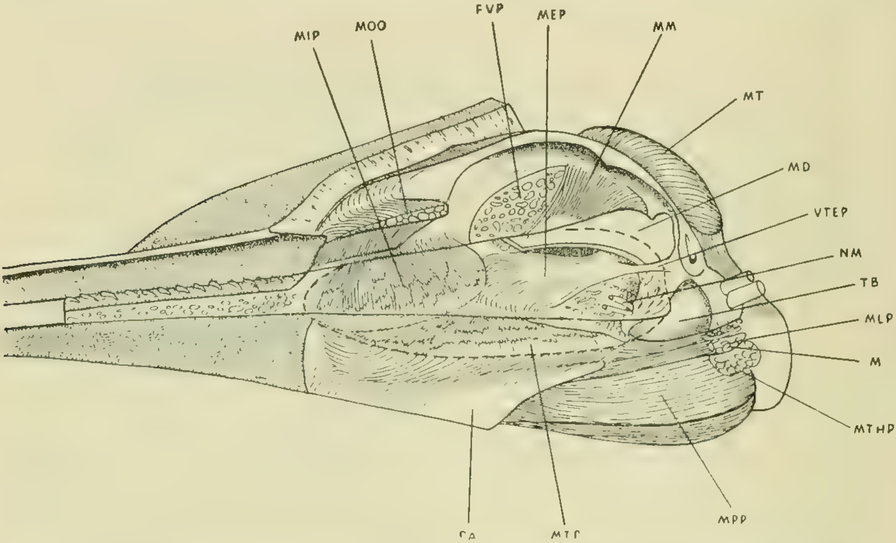

FIG. 4. Dissection of the left half of the head of *Delphinus delphis* to show interrelationships of palatal and pterygoid muscles. (Only the proximal end of the mandible is shown *in situ*, the remainder being indicated in outline.)

Common Dolphin it is elliptical in shape, the longer axis lying parallel to the long axis of the lower jaw.

Tensor palati muscle. The other portion of the ventro-lateral muscle mass referred to above is roughly of an acute angular shape, one side of the triangle lying along and overlapping the angular lateral edge of the pterygoid hamulus. Anteriorly it is attached along the whole posterior ventral margin of the palatine bone ; posteriorly to the lateral wall of the Eustachian tube and to the styloid near its junction with the tympanic bulla. Along the ventro-lateral edge of the pterygoid hamulus its muscle fibres run antero-mesially and merge into a strong, fibrous, glistening aponeurosis (PA) which covers the ventral surface of the palate and merges with the muscle of the opposite side. According to Boenninghaus, Zucherhandl wrongly identified this muscle as the tensor palati, but the present writers consider the latter author to be right (see p. 11). In *Delphinus delphis* the part of the mesial aspect of this muscle (MTP) is attached to the lateral wall of the pterygoid air sac posterior to the posterior margin of the lateral lamina of the pterygoid hamulus, whereas in *Mesoplodon bidens* the fascia of this muscle forms nearly the whole of the lateral wall of the pterygoid sac.

Between the postero-dorsal margin of this muscle and the postero-ventral margin of the external pterygoid muscle is a triangular space closed mesially by the fibrous supporting tissue previously mentioned, and pierced by the tensor palati and pterygoid branches of the mandibular nerve (NM).

According to Boenninghaus the tensor palati muscle is restricted to a few, small, inconspicuous, vestigial muscle fibres in the posterior nares close to the opening of the Eustachian tube. It may be pointed out that the muscle identified by the present writers and Zucherhandl as the tensor palati is innervated by a branch of the mandibular nerve, i.e. the conventional innervation of this muscle. The tensor palati of Boenninghaus is remote from this nerve and separated from it by the lateral wall of the posterior nares, the pterygoid air space and the lateral muscle mass.

Temporal muscle. Consideration of the temporal muscle (MT) is not within the scope of the present investigation. It need merely be said that it originates in the temporal fossa and passes through that portion of the zygomatic arch formed by the squamosal, to an insertion on the dorsal edge of the mandible posteriorly. Closely associated with, and situated ventrally to this muscle is another muscle mass which originates from the fibrous covering of the tympano-squamosal recess on the zygomatic process of the squamosal. It is inserted into the lateral face of the mandible and in its general position its identification as the masseter muscle (MM) seems reasonable.

Nasopharyngeal muscles. In order to demonstrate the manner in which the air sinus system has profoundly altered the arrangement of the muscles of the soft palate, it is necessary to review the inter-relationship of the components of the naso-pharyngeal muscle mass using *Delphinus delphis* (Text-figs. 3–6) as the subject. But before doing so it is well to recall the disposition in a typical mammal, for example man. According to Gray's *Anatomy* (1946) " the palatine aponeurosis (tendon of the tensor palati) forms a central sheet enclosing the uvular muscles near the median plane ; the levator palati and the palato-pharyngeus are inserted into its upper surface, the two strands of the latter muscle lying in the same plane respectively in front of and behind the levator palati." In Cetaceans, the dorsal and ventral surfaces of the palatine aponeurosis are widely separated by the expanded and distended hamular portions of the pterygoid bones and their associated air sinuses and venous plexuses (FVP). Thus in their narial portions the palato-pharyngeus and levator palati muscles (MPP) are separated from the ventral aspect of the palatine aponeurosis by the interval formed by the pterygoid air spaces. As a result of the development of these air spaces and the modifications of the pterygoid bones enclosing them, profound alterations of the conventional orientation of the naso-pharyngeal muscles have ensued. The "soft palate" is invaded by the pterygoid bones and is thus no longer soft, and the palato-pharyngeal muscle mass is largely enclosed within the bony nares (see Text-fig. 14*g*). The arrangement of this muscle mass in *Delphinus delphis* is almost identical with that so adequately described by Boenninghaus in *Phocaena phocoena* (see p. 11). Thus the partes interna and externa of the palato-pharyngeus muscles (MPP(I)) (MPP(E)) form the greater part of the thick mass of tissue which covers the anterior wall and floor of the posterior narial aperture, whilst the constrictor pharyngeus (MSC), salpingo-pharyngeus (MSP) and longitudinalis oesophagi (MLO) form the posterior portion of its roof. The ventral extremities of all these muscles encircle the glottis in a powerful palato-pharyngeal sphincter (MPP (S)).

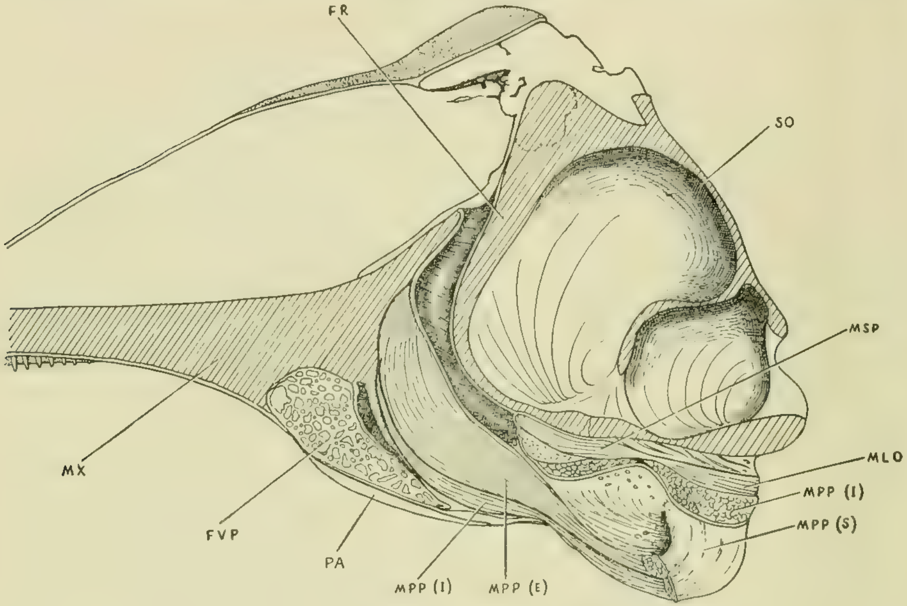

FIG. 5. Bisected head of *Delphinus delphis*, right side, showing naso-pharyngeal muscle mass *in situ*.

In Text-fig. 6. the whole palato-pharyngeal muscle mass has been removed from the nares to show that the individual muscles overlap in a manner similar to their arrangement in terrestrial mammals. The present writers, however, do not concur with Boenninghaus in his identification of the levator palati muscle, and consider that the muscle he so identified is merely a portion of the *pars interna* of the palato-pharyngeus. Indeed, Boenninghaus himself found it difficult to establish a differentiation of the two muscles. In *Delphinus delphis* (Text-figs. 4 and 6) there is a muscle (MLP) which arises from the junction of the styloid with the tympanic bulla, lies along the medial wall of the Eustachian tube, and after passing within the upper, concave border of the superior constrictor, runs dorsally between the partes interna and externa of the palato-pharyngeus ; thereafter it spreads out into the palatine glandular surface near the narial opening of the Eustachian tube. This

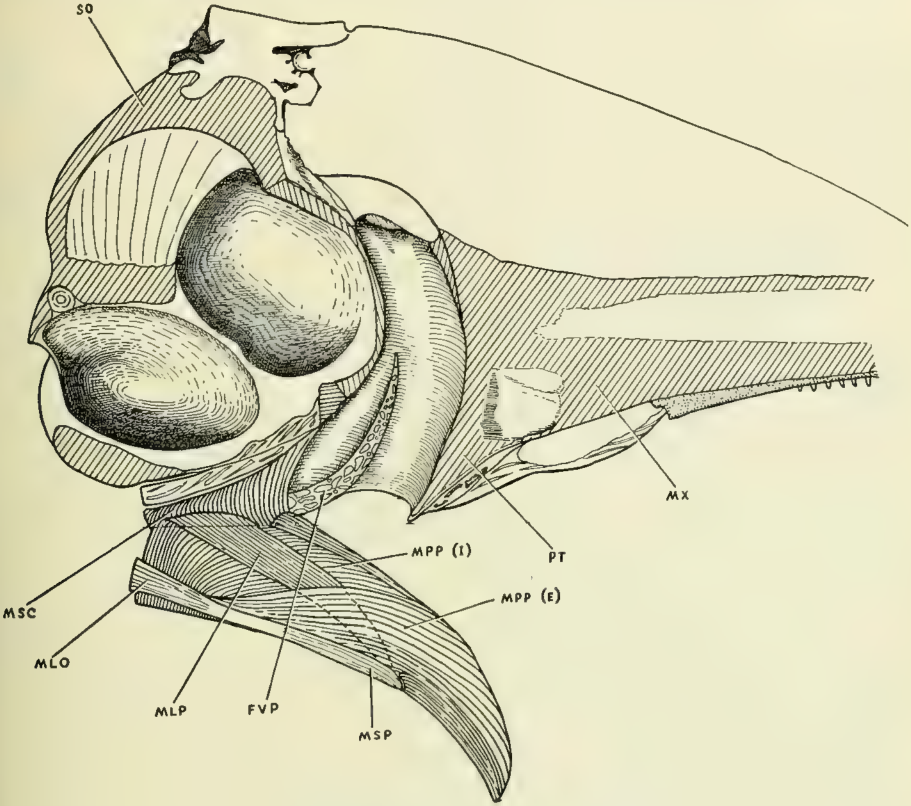

FIG. 6. Bisected head of *Delphinus delphis* left side, with naso-pharyngeal muscle mass reflected.

disposition of the muscle coincides in all its relationships with that identifying the levator palati in man.

(2) MESOPLODON

In the Ziphiidae the size and disposition of the lateral muscle mass are correlated with the enormously enlarged pterygoid hamuli (see Text-fig. 14*c*). It will be seen later that the air sinus system is almost wholly confined to this region, thus whilst the tensor palati muscle is expanded in correspondence with the enlargement of the hamuli, the expansion of each hamulus has apparently been at the expense of the remaining portion of the pterygoid, which is reduced to a long, narrow shelf, situated immediately above the hamular fossa. The " external " and " internal " pterygoid muscles extend from the upper surface of this shelf to the dorsal edge of the mandible and are consequently restricted to the narrow interval which separates these two attachments. The muscles are also flattened dorso-ventrally and in general are very much reduced in size, and presumably in function, compared with those of the Delphinidae. The temporal fossa, and with it the temporal muscle, is also reduced in size as compared with those of the Delphinidae.

(3) BALAENOPTERA

In order to complete the description of the musculature of the air sinus system, it is necessary to describe the arrangement in the baleen whales. Before doing so it may be noted that Beauregard (1894) identified in *Balaenoptera acutorostrata* a sheet of fibrous tissue covering the lower surface of the cranium, and closing the pterygoid sinus ventrally. This sheet is undoubtedly homologous with that described above (p. 12) in the Odontoceti.

With regard to the lateral muscle mass the writers have little to add to the description provided by Carte & Macalister (1869). They state " the pterygoid muscle was small and flat ; it arose fleshy from the external surface of the pterygoid plate, which formed the outer wall of the posterior nares ; the muscle ran downwards and backwards, and was inserted into the internal border of the lower jaw near its angle, sending some of the posterior fibres to be inserted into the interarticular fibro-cartilage. This muscle was evidently the representative of the external pterygoid ; no muscle corresponding to the internal pterygoid was found." In a dissection of a foetal fin whale the present writers were similarly unable to distinguish positively the internal pterygoid, but a small slip of muscle inserted into the mesial aspect of the lower jaw, approximately at the level of the coronoid process, appeared to have its origin in the lower part of the temporal fossa near or on the pterygoid bone. Its position relative to the lateral pterygoid suggested that it might be the internal pterygoid muscle.

The arrangement of the muscles in the naso-pharyngeal mass is precisely as in the Odontoceti except that the muscles are not enclosed within the bony nares (see Text-fig. 14*b*). This is related to the fact that the pterygoid hamuli do not extend towards the middle line and are not enormously enlarged as in the Odontoceti, a true soft palate persisting. It will be seen, from Carte & Macalister's description of the deep fibres of the masseter muscle which follows, that this muscle agrees in position and attachments with that tentatively so identified in *D. delphis* (p. 19 *supra*). They state " The deeper set of fibres arose tendinous from the margin of the glenoid cavity, extending as far forward as the posterior edge of the orbit ; the fibres of this plane ran downwards and a little forwards, and were inserted into the base of the lower jaw about three inches in front of its angle, and occupied by its insertion about three inches of the outer surface of this bone."

VASCULAR SYSTEM

The modification from the conventional arrangement of soft structures at the skull base with the development of air sinuses is particularly well demonstrated by the distribution of the blood vessels in this region. Anatomists such as Murie, Boenninghaus, Carte & Macalister have, with justification, described the blood vessels only in very general terms, because the ramifications of the finer branches are exceedingly complex and form extensive retia mirabilia which are associated with the air spaces. In order to relate their investigations with those of previous authors the present writers examined the vascular systems of five species of odontocete. Use was made of the recently developed polyester resins in order to obviate the necessity of making very laborious and less satisfactory dissections. The arterial and venous systems were injected with coloured plastic through the common carotid artery and jugular vein respectively. Freshly killed animals being unavailable, use was made of stranded specimens, the venous system of which naturally contained varying amounts of congealed blood. As a consequence the injection of this system was in some instances not complete, but sufficient information has been obtained by considering the injected specimens together to build up a composite impression. This impression is possible because inspection of the preparations of the heads of the five species injected, namely *Phocaena phocoena*, *Grampus griseus* (Text-fig. 7), *Tursiops truncatus* (Text-fig. 8), *Globicephala melaena* (frontispiece and Text-fig. 9) and *Lagenorhynchus albirostris* (Text-fig. 10) showed that the vascular system as a whole was very similar in each.

The general impression of the vascular system in the region of the base of the skull is of an elaborate plexus of vessels investing the whole of the air sac system, and apparently entirely subservient to the proper functioning of the latter. It is well known that the blood supply to the brain of cetaceans is by way of spinal meningeal arteries which are greatly increased in calibre and, correspondingly, the internal carotid is known to be reduced and apparently atrophied.

ARTERIAL SUPPLY

The external carotid (ACE) (Text-fig. 8) divides in the neighbourhood of the tympanic bulla into an external and internal maxillary artery, the former of these being irrelevant to the subject of this paper. The internal maxillary (AMI, Text-figs. 7, 8, 9, 10) can be referred to under the three sub-divisions recognized in terrestrial mammals.

The first part forms a sinuous curve and is enveloped in the superior portion of the intra-mandibular fatty tissue (IMFB); laterally it gives off the mandibular artery (AM) (Text-figs. 7, 8, 9) which is distributed to the ramus of the lower jaw.

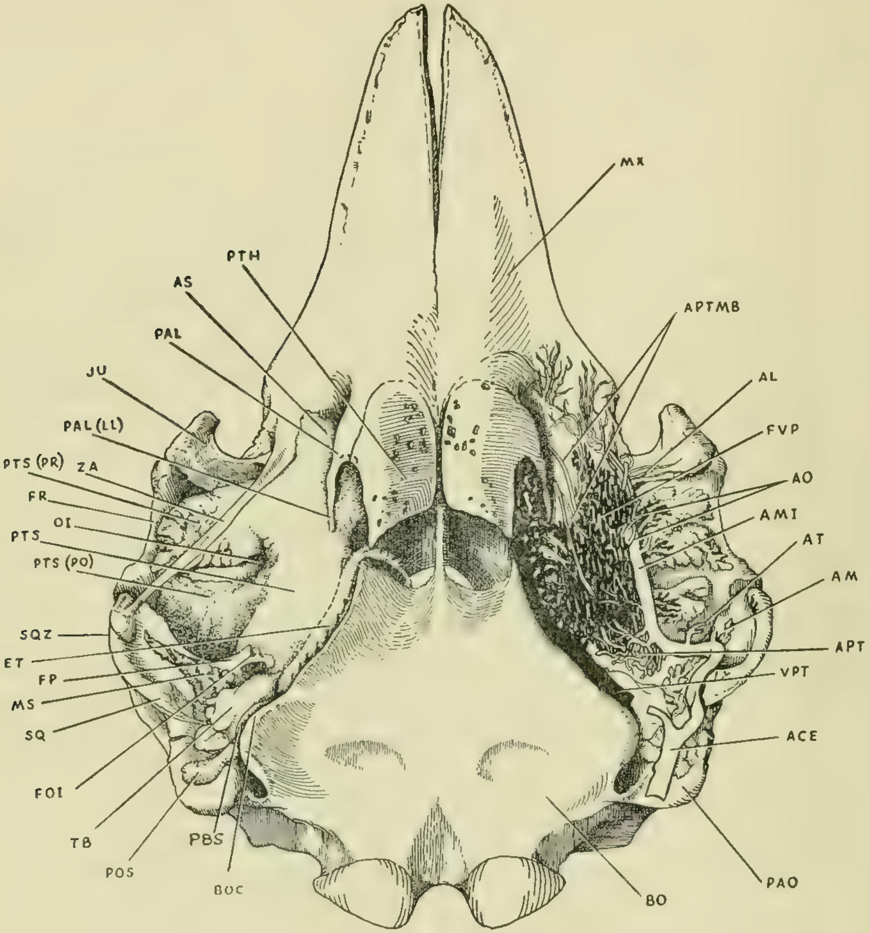
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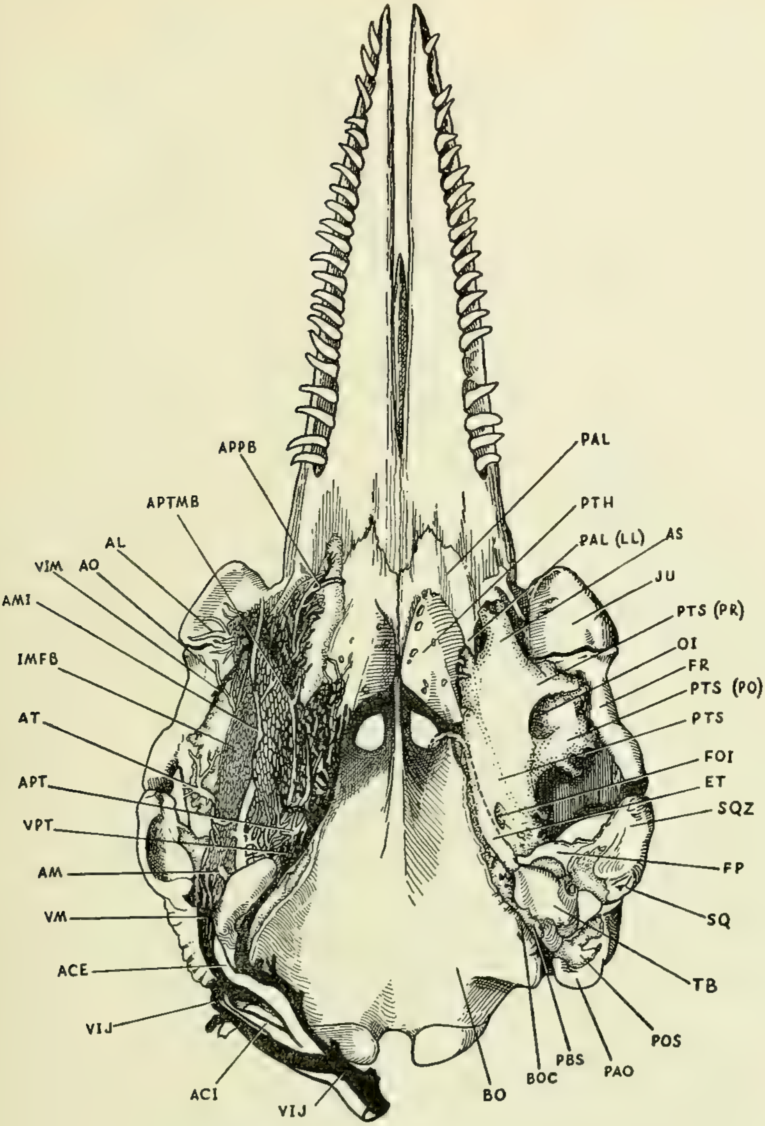
FIG. 7. *Grampus griseus.* Ventral aspect of the head showing distribution of air sinuses, arteries and veins.

Further forward it gives off, mesially, pterygoid arteries (APT) and laterally the deep temporal (AT) (Text-figs. 7, 8). The pterygoid arteries form a rich plexus of vessels which is distributed to the submucosa of the air sacs as well as to the external pterygoid and tensor and levator palati muscles. The plexus communicates


APPB
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PAL (LL)
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JU
PTS (PR)
OI
FR
PTS (PO)
PTS
FOI
ET
SQZ
FP
SQ
TB
POS
PAO
PBS
BOC
BO

FIG. 8. *Tursiops truncatus.* Ventral aspect of the head showing distribution of air sinuses, arteries and veins.

with the vascular envelope of the air sac system in the position of the angle formed by the tensor palati and lateral pterygoid muscles. The arteries supplying the internal pterygoid muscle (Text-figs. 7, 8, 9, 10, APTMB), although originating in approximately the same position as those supplying the external pterygoid, extend forward on a course approximately parallel with that of the parent (internal maxillary) vessel in conformity with the forward displacement of the internal pterygoid muscle (see p. 18).

In terrestrial mammals the middle meningeal artery is a conspicuous branch of the first portion of the internal maxillary, and anastomoses with the internal carotid. In at least one of the injected specimens evidence of an intra-cranial blood supply from this source has been established ; and it cannot be assumed that this artery has atrophied, notwithstanding the apparent atrophy of the internal carotid and the proliferation of the spinal meningeal supply.

The second part is not enclosed within any alisphenoid canal and indeed it is displaced from the lateral wall of the cranium by the whole width of the pterygoid air sinus. The vessels (AO and AL) stemming from this portion of the internal maxillary go to supply the orbital muscles, the lachrymal gland and upper eyelid (Text-figs. 7, 8, 9) ; their distribution is not relevant to the present paper but it may be noted that a considerable extent of main vessel separates the origins of the orbital and lachrymal branches.

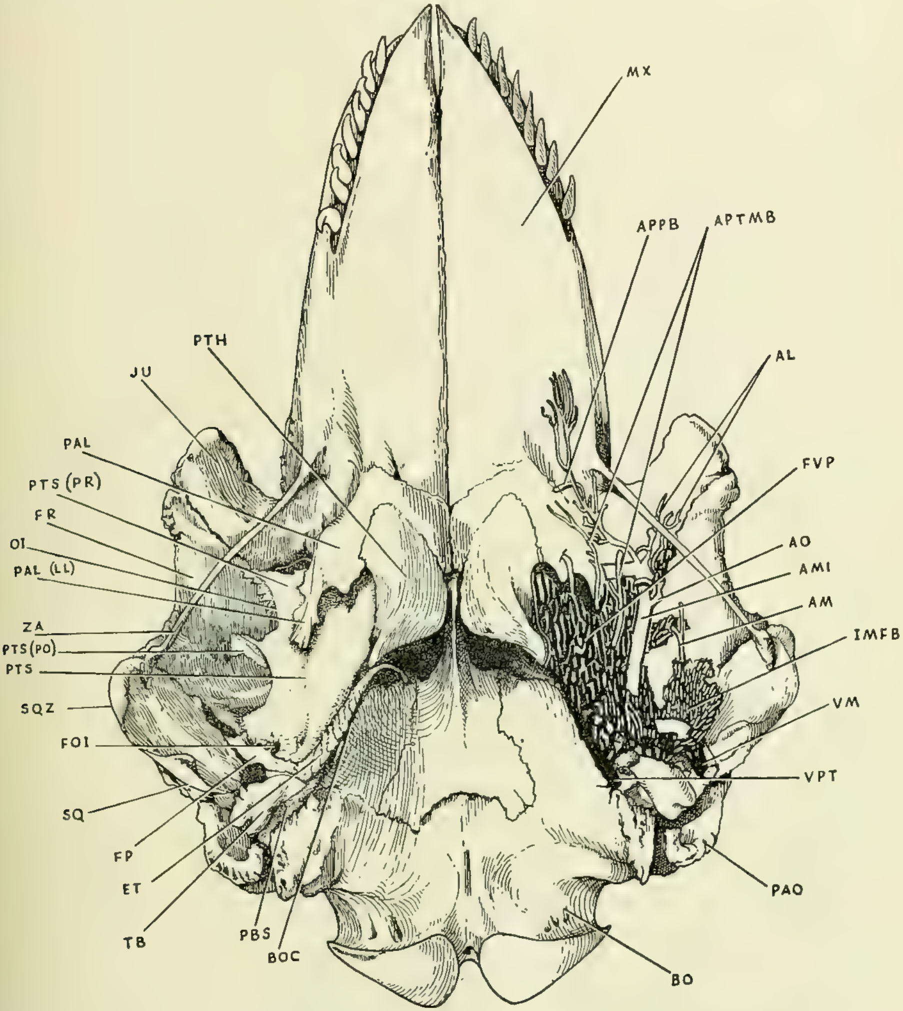
The third part commences immediately anteriorly to the lachrymal branch (AL) of the Second Part (Text-fig. 9). It immediately turns mesially and dorsally to pass through the infra-orbital foramen. Before doing so it gives off vessels, which penetrate the palatine base (Text-figs. 8, 9, APPB) presumably to supply the palato-pharyngeal muscle mass, and the roof of the mouth. Another branch ramifies on the ventro-lateral surface of the rostrum (Text-figs. 7, 9). The maxillary artery passes forward within the rostrum after giving off branches to the nasal cavity and the musculature of the blowhole. It is interesting to note that, as in the orbital region where the cranial foramina are crowded together, in the preorbital region the infra-orbital, spheno-palatine and posterior palatine foramina are all in juxtaposition.

VENOUS DRAINAGE

The venous drainage of the base of the skull is extremely complex and anastomoses freely with that of the cranial cavity. It is mainly characterized by the development of an extensive fibro-venous plexus which lines the whole of the lateral and mesial walls of the air sinuses. In spite of the profusion of retia, however, certain conventional features of the venous drainage can be recognized.

Internal maxillary vein. This vein (Text-fig. 8, VIM) can be said to commence at the posterior extremity of the zygomatic arch and pass forward parallel with the latter as far as the posterior margin of the jugal. It then passes over the dorsal edge of the ramus of the mandible and runs posteriorly in company with the artery (AMI) of the same name. In the temporal region it merges with the massive venous plexus of the intra-mandibular fatty body (IMFB), and is joined by the deep temporal vein.

Mandibular vein. Boenninghaus' identification of the intra-mandibular fatty body with the bone marrow of the lower jaw seems to be justified. A full description of its situation and extensions is given on p. 13. The venous plexus which ramifies extensively in the fatty body ultimately drains into a large vessel which can be recognized as the mandibular vein (Text-figs. 8, 9, 10, VM). The plexus consists primarily of a network of vessels of small calibre, the walls of which are extremely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PTS(PO)
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VM
FOI
VPT
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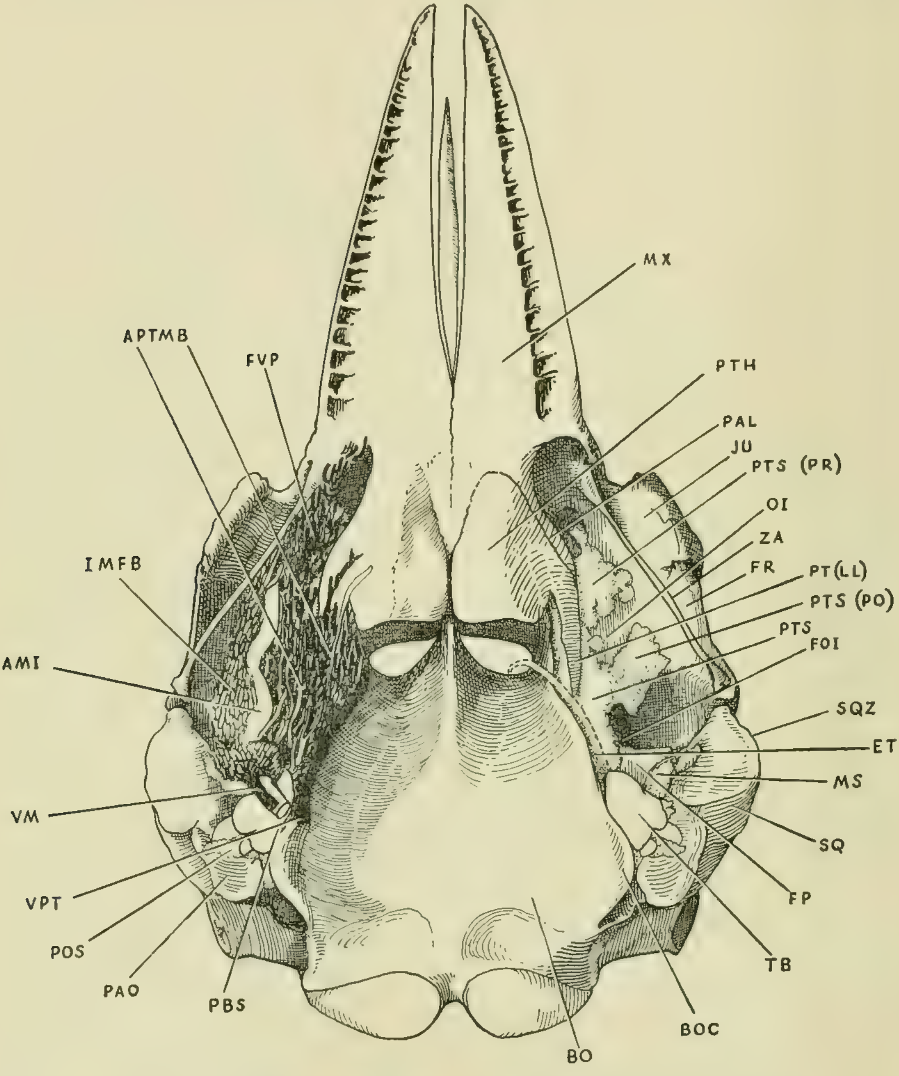
PAO
ET
TB
PBS
BOC
BO

FIG. 9. *Globicephala melaena.* Ventral aspect of the head showing distribution of air sinuses, arteries and veins.

thin and intimately associated with the adipose tissue of the marrow. Boenninghaus points out the tendency of the fatty body to hypertrophy beyond the natural boundaries of the mandible, and it is a significant fact that among the toothed cetaceans, even those with a reduced number of teeth, for example *Grampus griseus*,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AMI
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FIG. 10. *Lagenorhynchus albirostris.* Ventral aspect of the head showing distribution of air sinuses, arteries and veins.

have a greatly enlarged fatty body. The large size of the mandibular vein can be correlated with that of the large plexus it drains. It continues posteriorly beyond the postero-lateral border of the skull to join the internal jugular (VIJ).

Internal jugular vein. Like the internal carotid artery the internal jugular vein (Text-fig. 8) is short, sharply tapered and presumably reduced in function. It emerges from the paroccipital notch and accompanies the internal carotid artery posteriorly.

Pterygoid vein. Unlike that of terrestrial mammals the pterygoid vein (Text-, figs. 7, 8, 9, 10, VPT) in the Cetacea is not limited to the drainage of the pterygoidea. It is continuous with the great fibro-venous plexus of the air sacs so that its ramifications are co-extensive with the distribution of the sacs themselves. Thus there are portions of this plexus to be found in the post-orbital, orbital and pre-orbital regions of the head and in some species, e.g. *Delphinus delphis,* the plexus extends towards the tip of the rostrum. On the mesial aspect of the cranial portions of the air sac system the fibro-venous plexus communicates freely with extensions from the intracranial venous system, through the optic foramen, and by way of the cavernous, superior and inferior petrosal sinuses. As a result of the displacement of the tympano-periotic from participation in the wall of the cranium, the petrosal and cavernous sinuses are divested of their bony cranial protection and are anastomosed with the fibro-venous plexus (but see *Caperea* pp. 77–79). In the terrestrial mammals the internal carotid artery passes through the cavernous sinus within the cranial cavity. In the Cetacea it passes through the so-called cavernous tissue body within the tympanic cavity. It seems therefore that the problematical cavernous tissue body or spongy mass of Beauregard in the cetacean ear is the homologue of the cavernous sinus of terrestrial mammals. At the angle made by the tensor palati and lateral pterygoid muscles, the lateral portion of the fibro-venous plexus anastomoses extensively with the plexus of the intra-mandibular fatty body. The pterygoid vein passes posteriorly along the ventral margin of the basioccipital crest (BOC) and, according to Boenninghaus, at the level of the tympanic bulla (TB) is joined by small tributaries from the inferior petrosal sinus. Still further posteriorly it unites with the mandibular and internal jugular veins.

The schematic representation of the venous system described by Boenninghaus and reproduced in Text-fig. 2 agrees in the main with the arrangement found in the more recently injected specimens figured in the present paper. There are, however, certain modifications which are embodied in the diagram. Thus the vessel labelled "internal jugular" (6) is shown with a relatively wide lumen, whereas the injected specimens show that it is very attenuated at its cranial end (see Text-fig. 8). The vessel labelled "external jugular" (15) lies on the mesial side of the mandible and is more properly designated as the mandibular vein. As previously stated it is embedded in the plexus of the intra-mandibular fatty body. The vessel labelled "ramus bulbi venosi ad jugularem externam" (14) in the injected specimens consists of a mass of small vessels connecting the vascular plexus of the fatty tissue body to the "corpus fibro-cavernosum pterygoideum" (10) i.e. the fibro-venous plexus of the air sacs. No vessel corresponding to the "ramus bulbi-venosi ad jugularem internam" (13) could be found unless it be the deep temporal vein in which case it is not in direct communication with the fibro-venous plexus, since it drains the temporal muscle.

At the points of attachment of the pterygoid muscles to the walls of the air sacs. the vessels of the fibro-venous plexus are much smaller than those in areas where no muscles are attached.

No detailed dissection was made of the nervous system in the region involving the air sacs, but it might be expected that since the air sac system covers the ventrolateral aspect of part of the cranium the air sacs would be penetrated by the cranial nerves in this region. However, the paths of the nerves concerned are restricted to three exits, that associated with the optic infundibulum, that of the infundibulum of the foramen ovale and that of the "cranial hiatus" in the vicinity of the periotic.

CONTENTS OF THE AIR SACS AND HISTOLOGY

Foam

With reference to the contents of the pterygoid fossa, Brazier Howell (1930) writes "in freshly killed specimens this is entirely filled with a coarse foam of albuminous, rather than greasy texture. Whether this is so in living specimens cannot be demonstrated, but presumably it is, and the foam may have some function in determining the quality of sound reception."

One of us (P.E.P.) examined the pterygoid sinuses of approximately fifty pilot whales stranded at Dunbar (1950) and found that each one contained a similar type of foam.

Mr. D. E. Sergeant of the Newfoundland Fisheries Research Station, who had been asked to look out for this phenomenon, also noted its occurrence in a *Globicephala melaena* only 1½ hrs. after death.

Dr. R. M. Laws, National Institute of Oceanography, to whom a similar request had been made, reported that in no whale examined for this purpose was the foam lacking.

Dr. Robert Clarke of the same Institute, while at the Azores in 1955 examined a number of Sperm Whales in which foam was found to fill the pterygoid air sacs.

Histology

If the surface of the wall of the air sac is examined with the naked eye it is seen to be of a light brown colour and matt texture. This texture is the macroscopic expression of the presence of the openings of innumerable, minute ducts closely adjacent to one another with a separating, membranous network, the trabeculae of which are ca. 0·025 mm wide. Pl. 2, fig. A, shows a section cut in the plane of the surface of the mucous membrane. The ducts (DMU) are fairly uniform in size, their openings of a roughly oval shape and measuring approximately 0·2 mm at their widest diameter. In the thick part of the same section each duct is filled by a layer of inwardly projecting columnar cells (ECO), mucus and foreign particles. The longitudinal section (Pl. 2, fig. B) of the pterygoid sac lateral wall shows that these ducts communicate with an elaborate system of mucous glands (GMU) some simple, some racemose, some deeper than others. The glands are lined by a thick layer of columnar epithelium with goblet cells (Pl. 2, fig. C, GOC). The free surface of the interglandular areas of the mucous membrane is covered by ciliated epithelium (ECI). The whole glandular area is extremely vascular being equipped with an intricate network of capillaries and larger vessels.

The mucous membrane (MUM) is supported by a thick layer of fibrous tissue (Pl. 3, fig. A, TF) with here and there small clusters of fat cells (Pl. 3, fig. C, CF). The fibrous layer may also contain elastic tissue. Disposed at random throughout the tissue are circular spaces of small size, each bounded by a fine layer of brown, unstainable substance (Pl. 3, fig. C, FG), which presumably represent fat globules. A number of larger irregularly shaped spaces (Pl. 3, fig. B, LS) contain a filling of translucent, emulsoid texture (Pl. 3, fig. D).

Deep to the fibrous layer is an open network of large venous spaces (FVP) with interspersed arteries (A), and connected by strands of fibrous tissue (TF) and patches of fatty tissue (FT) (Pl. 3, fig. A). The boundaries of the venous spaces appear to be composed of the interlaced fibrous strands, no well-defined endothelium being present.

Another fibrous layer TF lies deep to the vascular plexus, attached to which can be seen many striped muscle fibres (MFS) (Pl. 3, fig. A) parallel with and closely adherent to the last named fibrous layer. In Plate 4, fig. A which is at right angles to the previous one a much larger area of this striped muscle (MFS) can be seen in transverse section, the peripheral regions of the individual muscle bundles being separated by fasciae originating from the fibrous layer (TF). The muscle involved is the external pterygoid.

The mucous membrane lining the mesial wall of the air sinus is identical in structure with that of the lateral wall. The photomicrograph of the sections (Pl. 3, fig. B) shows the membrane and its underlying structures. The crypts are rather more racemose than those of the lateral wall and, as in the latter, the sub-mucous layer is highly vascular, the cut ends of the vessels being seen in the sections. The circular and irregularly shaped spaces are also present. Below the mucous membrane, as in the lateral section, is a continuous layer of fibro-elastic tissue. Deep to this is a reticulation of the fibrous tissue containing very large venous spaces (FVP) with here and there arteries. This fibro-venous plexus is continuous with the haversian system of the mesial lamina of the pterygoid bone which is not represented in the sections.

In Fraser & Purves 1954 it is stated that the fibro-venous plexus referred to in the two previous sections was supplied by an arterial plexus which emerges from the internal maxillary artery immediately anterior to the tympanic bulla. The plexus is partially drained by an intricate plexus of small veins which penetrates the fibrous covering of the sinus at the angle formed by the lateral pterygoid and tensor palati muscles. This plexus is very dense and ramifies throughout the mass of fatty tissue which lies on the mesial aspect of the lower jaw. The section (Pl. 4, fig. B) is through the lateral wall of the air sac in this region. It is composed of mucous membrane (MUM) which as in the previous sections is provided with racemose crypts. The sub-mucous fibrous tissue (TF) contains considerable aggregations of elastic fibres arranged in sinuous folds. There are also numerous arterial capillaries

(A) and lymphatics. Deeper is a network of fibrovenous spaces (FVP) containing many large and small arterioles shown in transverse section. In places the fibrous interstices of the venous plexus are replaced by fat. Further laterally the fibrovenous plexus is continuous with a system of smaller venioles which penetrate a mass of adipose tissue, i.e. the fatty body of the lower jaw. The walls of these venioles are extremely thin.

Pl. 4, fig. C is a section from the intra-mandibular fatty body on the mesial aspect of the lower jaw showing reticulations of large venous spaces (VN). Open fat cells and lymph ducts are present. The section is lined at one side by a thin layer of fibrous tissue (TF)—mandibular periosteum (see p. 13 *supra*). It is interesting to compare this section with one taken from the fat layer on the lateral aspect of the lower jaw. In this section Pl. 4, fig. D the large venous spaces are absent, although normal arteries and veins are represented. The whole mass of tissue is streaked by parallel patches of striped muscle (MFS).

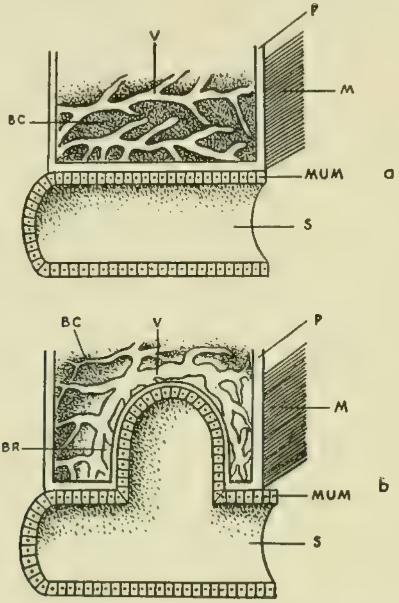

FIG. 11. Diagram to show formation of air sacs and fibro-venous plexus.

From these descriptions it can be seen that the lateral wall of the air sac is composed of four main layers :

1. Surface mucous membrane.
2. Thick layer of fibrous tissue.
3. Open plexus of veins and arteries.
4. A second band of fibrous tissue.

The foregoing histological description applies to the wall of the air sac however extensive the latter may be, so that the fibrous tissue sheet and vascular network mentioned by Boenninghaus reaches beyond the limits defined by him. It allows conclusions about its origin to be drawn. It will be seen in the next chapter that the sinus system is derived from a great extension of the limits of the pterygoid bone, and it is clear that the tissue sheet and vascular system are derived from the periosteum and osteo-vascular system of that bone in the manner shown in Text-fig. 11. Starting with a sinus (S) adjacent to a bone, which can be assumed to be the pterygoid (Text-fig. 11*a*) the principal features are a vascular system (V) in a bony matrix (BC) covered by a layer of periosteum (P), with, external to this again, the mucous membrane (MUM) which contributes the lining of an incipient air sinus system (S). A number of striped muscular fibres (M) are inserted into the lateral wall of the bone. In Text-fig. 11*b* an invagination of the pterygoid bone has commenced, with resorption of the calcified element (BC) of the bone. Laterally, where resorption has proceeded as far as the lateral aspect of the bone, a vascular system remains between two sheets of periosteum, the mesial component of which is lined by mucous membrane, and the lateral supporting the previously mentioned muscle fibres (M). Mesially in the sinus, resorption (BR) of the calcified element has not proceeded to the mesial limit of the bone so that the component parts of the wall of the sinus consist of a vascular network which is continuous with that of the bone, and covered laterally by a single sheet of periosteum and a layer of mucous membrane. The extent to which this process has developed in various cetaceans can be judged from the next chapter.

OSTEOLOGY

There are some features of the cetacean skull to which very little reference has been made in the relevant literature. As a preliminary to a description of these features in the various forms of cetacean it will be necessary to draw attention to basic aspects of the skull. Various descriptions exist of the more or less elongated rostrum, the overlapping extension of the maxillaries above or below the frontal, the elevation and enormous extension of the supra-occipital with the partial or complete exclusion of the frontal and parietal bones from the external surface of the cranium, the diminutive size of the nasal bones and the associated change in direction of the nasal passages from a horizontal to a dorso-ventral situation. The features which concern this paper however are to be found on the ventral aspect of the skull. They are :

1. The ventral displacement of the tympano-periotic bones and their dissociation from the adjacent bones of the cranium.
2. The presence of a falciform process of the squamosal.
3. The basioccipital crests which form a longitudinal arcade for the accommodation of the larynx and naso-pharyngeal muscle complex.
4. The disproportionate enlargement of the pterygoid with overriding of and intrusion into the palatine.

5. The splitting of the pterygoid, and sometimes of the alisphenoid and squamosal also, into lateral and mesial laminae, connected to a greater or lesser extent by superior and inferior laminae.

6. The excavation of the zygomatic process of the squamosal to form the tympano-squamosal recess.

In the descriptions of the skulls which follow, the osteological features will be discussed in the foregoing numerical order and the specimens will be considered in the following sequence—the Mysticeti including the Balaenopteridae, Balaenidae and Eschrichtidae; and the Odontoceti including the Ziphioidea, Physeteroidea, Platanistoidea, Monodontoidea, Delphinoidea.

MYSTICETI

BALAENOPTERIDAE

In the Mysticeti the arrangement of the bones in the region under discussion in the present paper are described and figured by Lillie (1910) who says " The Cetacea have a remarkable depression on the base of the cranium on each side of the median line (Lillie's fig. 71). In *Balaenoptera* these depressions are bounded posteriorly by the projecting edge of the exoccipital, externally by the base of the zygomatic process of the squamosal, on the inner side behind by the prominent edge of the basioccipital. The anterior portion of the inner side of this depression and the front of the recess are bounded by the pterygoid and alisphenoid bones which are fused together; the latter also form the roof of the anterior half of the depression. Thus the anterior portion of the cavity is bounded on three sides by the pterygoid and externally by the squamosal, and is known as the pterygoid fossa. In this recess the united tympanic and periotic bones lie."

Ridewood (1922) gives an extensive account of the pterygoid region of *Megaptera* and *Balaenoptera* in which he points out that Lillie's interpretation of the pterygoid fossa as being components of the pterygoid and alisphenoid was wrong, and that he confused it with the pterygoid fossa in man. In the latter the " lateral pterygoid plate " is the descending wing of the alisphenoid. Ridewood is in agreement with Van Kampen (1905) that the pterygoid fossa in mysticetes is contained within the pterygoid bone alone. This also is the interpretation accepted by the present writers and is substantiated by the evidence obtained from the Odontoceti.

The Mysticeti differ from the Odontoceti in that the tympano-periotic is not completely extruded from the cranial wall—thus there is no cranial hiatus. The pyramidal pro-otic portion projects into a cavity in the squamosal bone; the dorsal surface of the otic portion is a component of the ventral wall of the cranium; the opisthotic part forms a long thin extension which is the fused mastoid part of the periotic and tympanic. It lies in a deep groove between the exoccipital and the squamosal, its anterior face forming part of the boundary of the meatal groove.

Ridewood's (1922) description of the falciform process of *Megaptera* summarizes the condition found in Balaenopteridae generally (see Pl. 7, FP). He says " The front of the squamous portion (of the squamosal) is prolonged forward, inward and slightly downward as the bifid pterygoid process, the upper part of which overlaps the upper part of the pterygoid bone near, but behind and below the ala temporalis; the lower part of the fork, the processus falciformis, overlaps, i.e. lies external to the part of the pterygoid that forms the external boundary of the pterygoid fossa (or sinus). Between the two parts of the pterygoid just mentioned is a broad notch opening backward, which, in conjunction with the notch in the squamosal bone immediately above the processus falciformis, constitutes the foramen ovale" (see Pl. 7, FO). Later he states "It is unusual in mammals for the squamosal to extend so far forward as to reach the pterygoid; the whales are exceptional in this respect as they also are in having the foramen ovale in the form of a cleft between the squamosal and the pterygoid." It should be pointed out however that this cleft represents the external opening of the foramen ovale and communicates with a bony infundibulum as will be described in the Odontoceti. The cranial aperture of the infundibulum is formed by a notch in the alisphenoid, again as in the Odontoceti and emphasized in the Physeteridae.

The basioccipital crests (BOC), as shown in *Balaenoptera acutorostrata* (Pl. 7), are low and stout in comparison with the skull as a whole and with the condition found in the Odontoceti. They are insignificant in size. The paroccipital processes (PAO) on the other hand are very prominent and greatly extended laterally. The mesial part of the anterior margin of the process forms the posterior wall of a laterally directed groove, which is bounded anteriorly by the recessed posterior face of the mastoid process of the tympano-periotic (MAS).

In none of the Mysticeti does the pterygoid attain the proportions observed in odontocetes. The mesial (PT (ML)), superior (PT (SL)) and lateral laminae (PT (LL)) of the bone (see p. 34 *supra*) are complete, bounding the pterygoid fossa already referred to. The bony bridge which the lateral lamina of the pterygoid makes between the squamosal (SQ) and the palatine (PAL) is intact, so that the lateral wing of the alisphenoid is concealed except for a small part of its distal extremity in the temporal fossa. There is no extension of the pterygoid beyond the orbital region as in the Odontoceti.

The pterygoid hamuli (PTH) are very small, widely separated and not excavated. Because of this condition the palatine bones form an extensive part of the palate. They are long, broad laminae which posteriorly partly overlap the pterygoid.

There is no evidence of the presence of a tympano-squamosal recess (see p. 9 *supra*).

The extent to which the pterygoid process of the squamosal overlaps the pterygoid bone varies in different balaenopterids (Text-fig. 12 *a–e*). In *B. physalus* and *B. acutorostrata* a broad width of pterygoid separates the pterygoid process of the squamosal from the palatine. This width is progressively narrowed by the extension of the pterygoid process of the squamosal, in the order *B. borealis*, *Megaptera novaeangliae*, *B. brydei*, to *B. musculus* in which the process makes broad contact with the posterior margin of the palatine, so that in this last species the pterygoid is divided into two areas respectively ventral and lateral. It is interesting to note that the contact between squamosal and palatine achieved in *Balaenoptera musculus* is also to be seen in the odontocete *Pseudorca crassidens*.

BALAENIDAE. This family is represented by the two genera *Caperea* and *Balaena*.

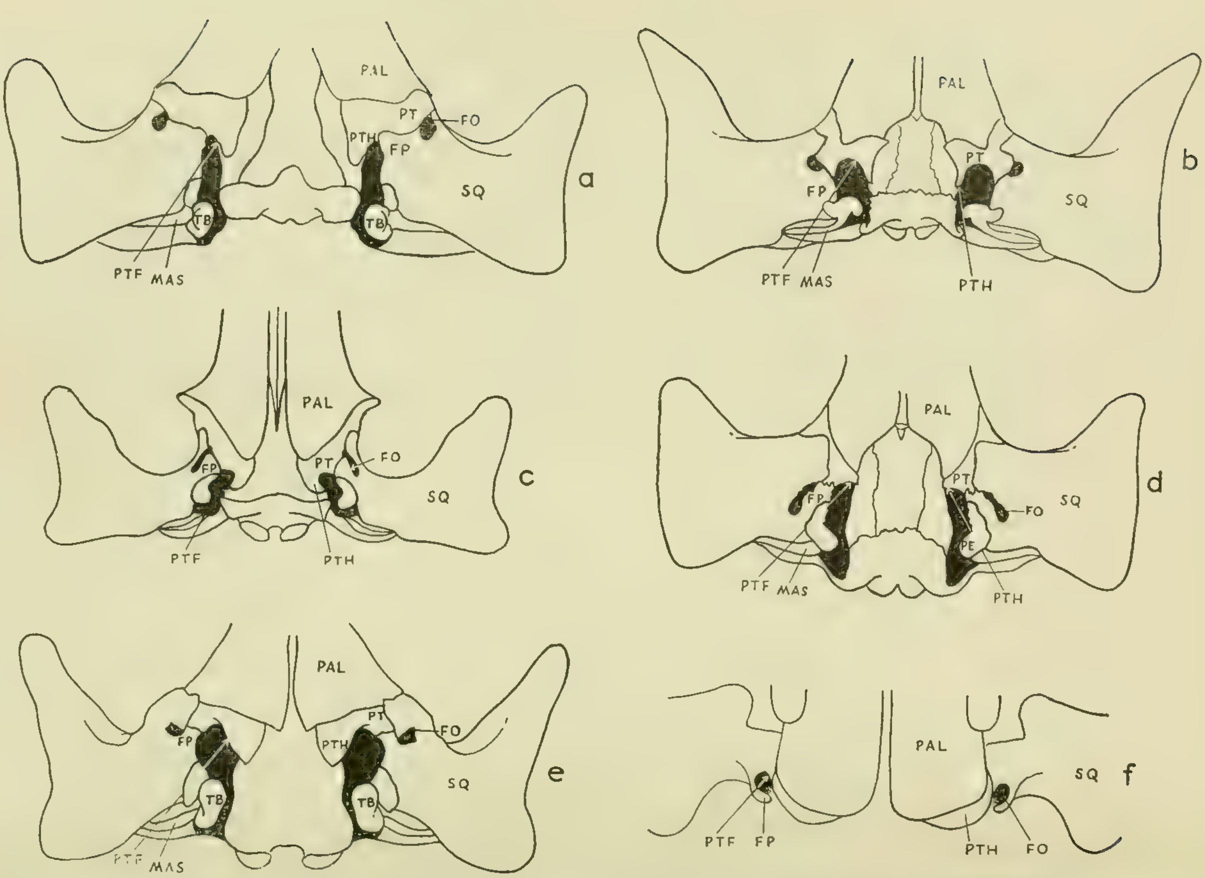
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FIG. 12. Diagrams to show relationship of the pterygoid to adjacent bones in various mysticetes.
a. *Balaenoptera physalus.* b. *B. borealis.* c. *M. novaeangliae.* d. *B. brydei.* e. *B. musculus.* f. *Balaena mysticetus.*

In respect of the parts under discussion in the present paper it shows the least degree of specialization. Referring to *Caperea marginata* first (Pl. 5 and 6), the skull as a whole shows more primitive features than any other mysticete. Neither the orbital process of the frontal nor the zygomatic process of the squamosal is very greatly extended laterally, the bony narial passages are elongated and there is a well-defined cribriform plate. The pterygoid hamuli (PTH) are inconspicuous and are separated from each other by nearly the total width of the choanae. The channel for the Eustachian tube from the tympanic cavity to the choanae is not merely a notch in the pterygoid but a deep antero-mesially-directed bony groove on the ventral aspect of the latter bone.

The tympano-periotic bones (TB and PE) are not entirely excluded from the wall of the cranium, a portion of the superior face of the periotic participating in the formation of the cranial cavity. The tympanic bulla is disproportionately large compared with the periotic and is itself relatively much larger than that found in any other mysticete. It is flattened ventrally to conform with the general level of adjacent bones and constitutes an appreciable part of the base of the skull in this region.

The mastoid processes of the tympanic and periotic are fused together, the relatively massive combined process extending to the lateral limit of the skull where it forms a roughly oval facet of considerable area between the basioccipital and squamosal. The mastoid process, although inserted between the bones just mentioned, is freely movable in the macerated skull.

With Ridewood's description of the falciform process of *Megaptera* in mind (see p. 34 *supra*) it should be noted that in *Caperea* the pterygoid process of the squamosal is not bifid and only that part of it corresponding to the falciform process (FP) is developed to any extent. It does not appreciably overlap the pterygoid bone except posteriorly and does not approximate to the external opening of the infundibulum of the foramen ovale (FO). This infundibulum is formed by a transverse, dorsally-directed bifurcation, the two branches of which meet dorsal to the infundibulum.

The basioccipital crests (BOC) are robust and unexcavated and approximate very closely to, but are not, as in terrestrial mammals, in contact with the mesial face of the bulla (see p. 77). The paroccipital process on each side is bounded mesially by a conspicuous semicircular notch which is much larger than, but corresponds in position with, the channel which conducts the 9th, 10th and 11th nerves as well as the internal carotid artery and the internal jugular vein. It communicates with a wide postero-lateral extension of the cranial cavity superior to the periotic. The paroccipital process is recessed on its anterior face to form the posterior limiting wall of an infundibulum, the anterior wall of which is provided by the posterior face of the mastoid process (MAS).

As in cetaceans, generally, the pterygoid bone of *Caperea* is split into a mesial (PT (ML)) and a lateral lamina (PT (LL)) but in addition, superior (PT (SL)) and inferior (PT (IL)) laminae are present so that the cavity so formed is only open posteriorly. The limited distention of the pterygoid sinus is indicated by (*a*) the antero-posterior width of the falciform process (FP), (*b*) the position of the mandibular branch of the 5th nerve (NM) which is anterior to the sinus of the pterygoid (see Text-fig. 15*b*).

It will be recalled that in *Balaenoptera* the infundibulum of the 5th nerve passes above, and posterior to the anterior limit of this sinus.

The pterygoid hamuli (PTH), in addition to being but poorly developed and widely separated, are quite remote from the excavated part of the pterygoids.

The pterygoid (PT) and palatine (PAL) bones meet in a simple edge-to-edge suture, there being no over-lapping of the pterygoid by the palatine as in the Balaenopteridae, and of the palatine by the pterygoid as in the Odontoceti.

There is a deep fissure between the glenoid process and the pterygoid which is comparable in position with the tympano-squamosal recess of odontocetes, but its association, as in odontocetes, with the system of tympanic air spaces seems unlikely. It evidently appears to be related to the close proximity of the elongated glenoid process with the distended lateral lamina of the pterygoid.

The members of the genus *Balaena* although, generally speaking, not as specialized as the Balaenopteridae, still show a considerable advance on the conditions found in *Caperea*. Both the orbital process of the frontal and the zygomatic process of the squamosal are greatly extended laterally. The paroccipital process shows less lateral extension than in the Balaenopteridae. The hard palate is extended posteriorly, the palatine bones being squamous over the pterygoid hamuli to an extent that the latter are sometimes completely hidden in the ventral view of the skull (Text-fig. 12*f*). (The Balaenidae in this condition thus demonstrate exactly the reverse of the condition found in *Platanista* in which the greatly extended pterygoids completely cover the palatines). The hamuli themselves are better developed than in *Caperea*. Their greatly flattened ventral surfaces are in apposition to the overlying palatine bones and the posterior portions of their mesial borders extend towards the middle line.

The tympano-periotic bones are withdrawn in a ventral direction from the cranial cavity, being separated from the latter by a long, narrow, antero-mesially directed infundibulum (Text-fig. 13*c*). The combined tympanic and periotic pars mastoidea is more attenuated than in *Caperea* but considerably shorter than in any of the Balaenopterids, this being associated with the state of development of the paroccipital process. It bears a facet which is a component part of the external surface in this region. The pyramidal pro-otic portion of the periotic is widely exposed and not partly overlapped by the squamosal as in the Balaenopteridae. The tympanic bullae are relatively large and are flattened dorso-ventrally as in *Caperea*. As in the latter their ventral faces form an important portion of the postero-ventral surface of the skull. Their mesial borders approximate closely to the lateral margins of the basioccipital crests.

The pterygoid process of the squamosal is bifid as in the Balaenopteridae but is directed postero-ventrally instead of antero-ventrally as in the latter family. The process overlaps the pterygoid and bifurcates round the external aperture of the foramen ovale forming posteriorly a well defined falciform process (Text-fig. 12*f*, FP). The infundibulum of the foramen ovale (FO) is incomplete posteriorly since the superior lamina of the pterygoid bone is not extended posteriorly as in the Balaenopteridae.

The basioccipital crests are very stout and roughly pyramidal in shape, and are overriden to some extent anteriorly by squamous extensions of the otherwise equally robust mesial laminae of the pterygoids. Each paroccipital process, as previously stated, is relatively short. At the mesial end of its antero-ventral surface is a short, elongated, oval concavity which is in juxtaposition with a similar concavity on the postero-dorsal face of the " pars mastoidea " of the tympano-periotic.

The pterygoid bones, as in other cetaceans, are split into mesial and lateral laminae to form the so-called pterygoid fossa. The two laminae are continuous ventrally and anteriorly, but the superior lamina is deficient posteriorly so that part of the alisphenoid adjacent to the path of the mandibular branch of the fifth nerve is visible in the roof of the pterygoid fossa. The orbital portions of the pterygoid bones are for the most part concealed by a dorso-lateral extension of the palatine. A small slip of the pterygoid can, however, be seen adjacent to the alisphenoid-squamosal suture. The pterygoid hamuli, already described, are not excavated.

The squamosal has an even wider contact with the palatine than in *Balaenoptera musculus* (Text-fig. 12*f*). Between the pterygoid process of the squamosal and the glenoid process (the latter of which is greatly extended ventrally) is a deep concavity which is in the position of the tympano-squamosal recess of the Odontoceti but it is not to be considered homologous with the latter.

ESCHRICHTIDAE. In *Eschrichtius*, as in other cetaceans, the tympano-periotic bone is dissociated from the remainder of the skull and its relation to the cranial cavity is as in *Balaenoptera*. The thin, laminate mastoid process is inserted between the squamosal and basioccipital and extends to the lateral limit of the latter bone. The falciform process is slender and more attenuated than in *Balaenoptera*, resembling in this respect *Balaena*, but it is directed antero-ventrally as in *Balaenoptera*. The infundibulum of the mandibular branch of the 5th nerve is open to the tympanic cavity and occupies the same position as in *Balaena*.

The basioccipital crests are not very prominent but extremely robust with little excavation of their lateral faces. As in *Balaena* the paroccipital notch is very wide, and a smooth area in its proximity suggests excavation of the bone in this region.

The laminae of the pterygoid are complete but the superior lamina does not extend posteriorly under the 5th nerve infundibulum as it does in *Balaenoptera*. The pterygoid fossa does not extend anteriorly as far as in *Balaenoptera* but the pterygoid hamuli are similar in shape to those of the latter species, being unexcavated and not dorso-ventrally compressed as in *Balaena*. The amount of backward extension of the palatine bones in *Eschrichtius* is midway between *Balaenoptera* and *Balaena*.

It will thus be seen that *Eschrichtius* occupies an intermediate position between *Balaena* and *Balaenoptera* as far as the pterygoid sinus system is concerned.

ODONTOCETI

ZIPHIOIDEA

The following species of ziphioid whale have been examined—*Hyperoodon ampullatus*, *Berardius arnuxi*, *Berardius bairdi*, *Ziphius cavirostris*, *Mesoplodon bidens* (Pls. 8–12). Two general features emerge from the examination, the first being the distinctive difference between the Ziphioids and the Delphinids of the regions under discussion in this paper, the second being the general homogeneity and smoothness of structure of this region in all the ziphioids, there being little or no evidence of progressive changes between individual species.

The tympano-periotic bones of the Ziphioids are excluded from the wall of the cranial cavity, but unlike that of delphinids the mastoid process of the tympanic (MAS) is relatively larger and interdigitates with the pars mastoidea of the squamosal. This interdigitation has been described by many authors as an actual fusion of the bones concerned but in no specimen examined by the present writers has fusion been observed ; in the macerated skull, whatever the age of the animal concerned, the mastoid process of the tympanic is always freely moveable. In very young specimens there is a cranial hiatus dorsal to the periotic but this is soon occluded by extensions of the bones adjacent to the hiatus.

The falciform process (FP) is invariably in the form of a stout spine curving round the anterior margin of the tympanic bulla (TB) and in close approximation to the latter. The process in *Ziphius cavirostris* is distinctive in being stouter, more robust and more flattened meso-laterally than in the remainder of the species examined.

A considerable portion of the proximal part of the infundibulum of the foramen ovale (FO) is present as a lamelliform shelf forming the ventral wall of the channel.

The basioccipital crests (BOC) are massive and show no cavitation of their lateral aspect. The interval between the tympanic bulla and crest is very narrow. The peribullary space as a whole is extremely restricted, and there is none of the excavation round the dorsal margin of the foramen ovale which occurs in the Delphinoidea. The paroccipital processes are massive, unexcavated tubercles. The extensive interdigitation of the mastoid process of the periotic with the paroccipital process is probably associated with the absence of excavation of the anterior face of the latter.

The pterygoid bones are conspicuously large, their length being about one third that of the skull. The general form of the pterygoids is such as to suggest a fundamental difference in the process of modification of these bones in the Ziphioidea from that of all other cetaceans in the disproportionate development of the hamulus (PTH). It will be seen below that in *Platanista* each pterygoid bone is split longitudinally, and more or less equally, into a mesial and a lateral lamina, and that the process of modification from this simple form throughout the series of skulls described, consists of a gradual distention and elaboration of the inter-laminar space, together with the formation of a superior lamina.

In the absence of intermediate stages between the primitive form of pterygoid and the more or less uniform resultant form found in recent ziphioids, the writers' interpretation of the mode of formation of the pterygoid bones is as follows. There appears to have been an initial splitting of the pterygoids, but thereafter this has progressed very asymmetrically, so that the mesial lamina is enormously enlarged whilst the lateral lamina is relatively inconspicuous and compressed ventro-dorsally, and is horizontally instead of vertically disposed. In this condition it overlaps the alisphenoid (ALS), orbitosphenoid (OS) and part of the palatine (PAL). The result of the great exaggeration of the mesial lamina is that the pterygoid hamulus (PTH) is disproportionately enlarged and distended posteriorly and anteriorly. The great fossa on the lateral aspect of the pterygoid bone can be said to be made up almost entirely of the hamular part of the bone, the posterior tip of which is extended backwards to the level of the anterior margin of the basioccipital crest, emphasizing the acuity of the pterygoid notch. Anteriorly the pterygoid bone extends forward over the palatine to make contact with the maxilla (MX) thus dividing the palatine into mesial and lateral portions. In this region the lateral and dorsal parts of the pterygoid are frequently of extreme thinness and in places the bone as such has altogether disappeared, exposing the underlying palatine in macerated specimens (see Pl. 9). The asymmetrical evolution of the pterygoid fossa probably accounts for the greater robustness of the hamuli as compared with those of the delphinoids. In the specimens of *Berardius bairdi* and *B. arnuxi* examined, that part of the pterygoid overlying the alisphenoid is also rarified so that part of the ventral surface of the latter bone is exposed.

The tympano-squamosal recess (TSQR) is of the form found generally in other odontocetes but its boundaries are not as well defined. It consists of a posterior portion which occupies the region behind the glenoid fossa and an anterior extension which lies mesial to the latter fossa and along the anterior margin of the zygomatic process of the squamosal.

Physeteroidea

In *Kogia* (Pl. 16) as in the ziphioid whales the tympano-periotic bones are excluded from the wall of the cranial cavity, and the mastoid process of the periotic (MAS) is much larger than in the delphinoids. The tympano-periotic bones are apparently disproportionately small, but the mastoid process of the periotic is relatively much larger than in the ziphioids and does not interdigitate with the pars mastoidea of the squamosal. It is a stout, roughly pyramidal tubercle of which the apex points towards, and is attached to, the periotic, and of which the base forms its external aspect. On its squamosal face the bone is marked by a series of deep, radiating channels which appear to be connected with the peculiar cancellated structure of the bone. Its paroccipital aspect forms a smooth, triangular facet. There are no marks on the squamosal nor on the paroccipital process which would suggest a close articulation. On the contrary, the mastoid process appears to lie quite loosely between the bones adjacent to it. When the pars mastoidea of the periotic is dissociated from the latter it is extremely light in weight, is translucent and floats in water as if pneumatized. The mamillated appearance of the external surface of the bone is extremely reminiscent of that of the pneumatized squamosal of other mammals (e.g. adult gorilla). It may also be noted that in the ziphioids generally, as well as in *Kogia*, the bone in the mastoid region has a peculiar, crevassed appearance quite distinct from the bone adjacent to it.

There appears to be no trace of a falciform process, the articulation of the squamosal (SQ) with the alisphenoid (ALS) being more like that found in terrestrial mammals. The foramen ovale (FO) is also in the position typical of terrestrial mammals, that is, within the alisphenoid bone, and there is no trace of a bony infundibulum such as is found in most of the delphinids.

The basioccipital crests (BOC) are stout and prominent, and the paroccipital processes are very large and their concavities of a size commensurate with that of the massive mastoid processes of the periotic.

The pterygoid bones are very greatly enlarged, their length being between a half and two-thirds that of the skull. The constitution of the pterygoid bone is interpretable in terms comparable with those used in connection with the ziphioids, that is to say the splitting of the pterygoid plate appears to have taken place asymmetrically, the mesial lamina (PT (ML)) being greatly enlarged. The ventro-dorsally compressed superior lamina (PT (SL)) is represented only by a short shelf of bone extending laterally below the orbito-sphenoid. It will be recalled that in the ziphioids the greater part of the pterygoid distention was in the hamular region. The reverse is the case in *Kogia*, the hamulus (PTH) being relatively insignificant and not at all distended, whilst the mesial lamina is grossly enlarged and extended posteriorly, partially to override the basioccipital crest. The effect of this on the position of the foramen ovale is discussed in the section below dealing with *Physeter*. Anteriorly the pterygoids are extended as squamations which make contact with the maxillae (MX) and divide the palatines (PAL) into mesial and lateral areas.

The greater part of the ventral surface of the orbital process of the frontals (FR), as well as the preorbital portions of the maxillae have a characteristic smoothness.

The tympano-squamosal recess is poorly developed, consisting of a single lobe which lies along the posterior border of the zygomatic process of the squamosal and terminates at the mesial limit of the ill-defined glenoid fossa.

Flower (1868) remarks on the small size of the tympano-periotic bones of *Physeter catodon*. He goes on to draw attention to the development of a large mass of curiously laminated bone which he says extends from the posterior and outer end of the tympanic, close to its attachment to the periotic, and thicker at its distal than at its proximal end. He states that it is composed of a large number of distinct, thin plates held together only by their common attachment to the tympanic. The present writers have been able to distinguish only two such plates which they regard as the tympanic and periotic elements of the mastoid process. This condition can be homologized with that found in the Delphinioidea, in which, to quote Flower himself : " This process resembles in its relations the mastoid of ordinary mammals, but in young cetaceans it may be seen to be composed of two nearly equal parts, in close apposition with each other, the inferior being derived from the tympanic and the superior from the periotic so that the latter alone can represent the pars mastoidea of other mammals." As Flower says, referring again to the Sperm Whale : " The whole mass partly overlaps and embraces the hinder edge of the squamosal and partly fits into a groove between the latter and the exoccipital." He goes on " It evidently corresponds to the strong tenon-like process of corresponding situation and function in the Whalebone Whales". " The contiguous edge of the squamosal has a laminated character, the ridges and grooves on its surface exactly fitting those of the appendage of the tympanic " [i.e. tympano-periotic].

In the skull of a female sperm whale examined, the mastoid process is not firmly wedged, but freely movable between the bones adjacent to it. The ventral edge of the process is strongly involuted so as to form a bony canal for the external meatus.

The tympano-periotic bones are excluded from the wall of the cranium and in the specimen examined, no trace of the cranial hiatus remains.

The falciform process is moderately well developed, in this respect differing from *Kogia*. The foramen ovale is displaced anteriorly from the process by a considerable distance, a feature to which reference will be made below, and in which *Physeter* and *Kogia* differ from all other cetaceans.

The basioccipital crests are massive tuberosities and are very short antero-posteriorly. The paroccipital processes are relatively small and the ventral margin of the lateral border is strongly involuted to form an infundibulum, the inner end of which is continued in a groove giving access to the peribullary space. As in *Kogia* the pterygoid bones are relatively large and appear to have undergone the same process of asymmetrical splitting observed in the ziphioids. The lateral lamina is extremely compressed ventro-dorsally and squamated over the alisphenoid, orbito-sphenoid and frontal bones. The distention of the pterygoid hamulus is slightly greater than in *Kogia* but this part is relatively insignificant as compared with the mesial lamina. The lateral lamina is extended ventrally and posteriorly so that it overrides and partially envelops the basioccipital bone. By the same process the pterygoid notch is deepened but diminished in size. This process of extension posteriorly seems to have involved the posterior margin of the alisphenoid bone.

In the foetal specimen of this species the foramen ovale is situated at the end of a conspicuous longitudinal notch in the posterior margin of the alisphenoid. In the adult specimen the foramen ovale is still more anteriorly situated, and even although it appears to penetrate the lateral wing of the alisphenoid, its true relationship is with the closed up, re-entrant portion of the posterior margin of the latter bone, as in the above-mentioned foetal specimen and in cetaceans generally. The longitudinal notch in the posterior border of the alisphenoid is clearly visible in adult specimens of *Kogia*.

The pterygoid bones are not squamated over the palatines to the same extent as in *Kogia*, the latter bones not being divided into mesial and lateral areas. The whole of the base of the cranium external to the pterygoids shows extensive squamation and rarification of the bones involved.

The glenoid fossa is ill-defined, to say the least, so that it is impossible to delineate the boundaries of the tympano-squamosal recess, but most of the ventral aspect of the zygomatic process of the squamosal is of a characteristic smoothness and has its antero-mesial margin squamated over the alisphenoid.

PLATANISTOIDEA (Pls. 17–23)

Contrary to the view of Hyrtl (1845), repeated by Yamada (1955), the tympano-periotic of *Platanista* (Pls. 17, 18) is not fused to adjacent elements of the cranium in any of the specimens in the British Museum collections, and the series includes old as well as juvenile skulls. The mastoid process (MAS) of the periotic is intimately interdigitated with the squamosal so that after maceration the tympano-periotic remains *in situ* but is freely movable in its interlocked position. The combined elements are displaced ventrally and somewhat laterally from the cranial cavity and the hiatus in the cranial cavity thus formed is partially filled by osteosclerosis of the squamosal, parietal and occipital.

The falciform process (FP) is a stout, bony plate which passes antero-ventrally round the posterior border of the foramen ovale (FO,) almost covering over the alisphenoid and making contact with the posterior border of the lateral lamina (PT (LL)) of the pterygoid bone. There is thus a complete bony bridge extending from the maxilla (MX) to the squamosal (SQ).

The basioccipital crests (BOC), although not very prominent, are stout in structure and on their lateral (tympano-periotic) aspect are profusely cavitated in a manner reminiscent of the mastoid region of terrestrial mammals. Posteriorly to the crests the paroccipital processes (PAO) are deeply excavated by narrow, dorsally-directed concavities.

The palatines are completely obliterated from view by the forward extension of the laminae of the pterygoids. External to the basioccipital arcade, the anterior portion of the squamosal, the alisphenoid and pterygoid bones are split into two distinct laminae with an interval between which is crossed by bony trabeculae and is continuous with the tympanic cavity. The passage of the mandibular branch of the trigeminal nerve through the foramen ovale traverses the inter-laminar space in the form of a bony tube. There is reason to believe that the inter-laminar space (ILS) communicates with another similar inter-laminar space occupying the whole of the mesial aspect of the massive maxillary crests (MXC) which characterize the gangetic Dolphin.

In all the British Museum specimens of *Platanista* except that shown in Pl. 18 the hamular processes of the pterygoids (PTH) are missing and skulls are generally depicted without them. Pl. 18 shows that well-defined processes are present in the juvenile and that they meet in the middle line. They are excavated like the remainder of the pterygoid bones and the ventral surfaces show extensive fenestration. It seems likely that the processes persist in the adult but that they are usually lost in maceration.

In the posterior, proximal part of the zygomatic process of the squamosal there is a ventrally situated, deep, triangular recess the posterior angle of which is adjacent to, and confluent with, the petro-tympanic fissure, the tympano-squamosal recess (TSQR). The ventral angle occupies the mesial aspect of the glenoid process which is deeply excavated. The lateral borders of this recess are strongly involuted. The position and extent of the recess and its contiguity with the petro-tympanic fissure recall the pneumatic extension of the tympanic cavity of *Macropus* as described by Owen (*Anat. of Vert.* Vol. II, p. 341).

In the specimen of *Stenodelphis* figured (Pl. 19), the tympano-periotic is missing but its absence serves to demonstrate the process of exclusion from the cranial cavity already referred to in *Platanista*. The large hiatus (CRH) in the cranial wall can be seen to be partially filled in by osteosclerotic extensions of the alisphenoid (ALS) and parietal (PAR) bones.

As in *Platanista*, the falciform process (FP) is wide, overlaps the alisphenoid and anteriorly makes contact with the posterior border of the pterygoid bone.

The downward extension of the basioccipital crests (BOC) is more emphasized than in *Platanista*. The bone substance does not show the characteristic cavitation seen in *Platanista* except in the region of the paroccipital processes (PAO) which are excavated in a manner comparable with that in the last named genus.

The pterygoid bones do not quite cover the palatine bones (Pl. 19, PAL) but laterally they have an anterior extension below the orbit as far as the jugal (PT and JU). Anteriorly to the tympanic cavity the interlaminar space of the pterygoids is more distended than that of *Platanista*. The bony connection between the lateral and mesial openings of the foramen ovale (FO) is deficient ventrally and laterally. The lateral lamina of the pterygoid (PT (LL)) shows extensive fenestration and antero-laterally the interlaminar space continues into the mesial end of the orbit. The two pterygoid hamuli (PTH) are distended meso-laterally but unlike those of *Platanista* their mesial borders are not in contact but form a wide angle. Anteriorly the dorsal and ventral extensions of each pterygoid are separated by a wide, plate-like process of the maxillary bone (MX).

The orbital extension of the pterygoid bone is of great significance in the interpretation of the distribution of the air sacs in other cetaceans.

The tympano-squamosal recess (TSQR) in the vicinity of the glenoid fossa is more extensive in *Stenodelphis* than in *Platanista*. It can be associated morphologically with the latter by regarding the anterior angle as being much extended anteriorly along the mesial border of the zygomatic process of the squamosal (SQZ). In its course this part of the recess curves round, and in part overlies, the glenoid fossa. Its anterior extremity is situated slightly anterior to the notch formed by the junction of the zygomatic process with the lateral wall of the cranium.

In the genus *Inia* resorbtion of the bones under discussion has proceeded to such an extent that interpretation of their arrangement has had to be arrived at with reference to X-ray photographs of the air sinuses. In Pl. 21 the tympano-periotic is wanting but its absence permits to be seen the same process of exclusion of the ear-bones from cranial contact that was observed in the previously described genus. The osteosclerotic parts of the squamosal, parietal and basioccipital can be seen in the figure forming the anterior margin of the cranial hiatus (CRH).

The falciform process (FP) is reduced to a low, acutely-ridged eminence extending posteriorly from the squamoso-alisphenoidal suture.

At the anterior border of the foramen ovale (FO) an acutely-pointed, laterally-directed process represents the remaining vestige of the bony tube[1] which in *Platanista* connects the cranial and external apertures of the foramen.

The basioccipital crests (BOC) are moderately prominent but rather thin and plate-like. This condition in *Inia* may be interpreted as being due to the merging of numerous cavities like those observed in this region in *Platanista*. The same explanation would account for the deep, re-entrant angle that the plane of the crest makes with the portion of the basioccipital in the vicinity of the tympano-periotic.

Of the hollow which occupied the paroccipital process (PAO) of *Platanista* and *Stenodelphis* only the posterior boundary remains in *Inia*. The anterior and mesial delimitations have completely disappeared so that the cavity persists only as part of the peribullary space.

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[1] In the succeeding references to the bony tube it should be noted that in the plates the presence of its osseous remnants is usually obscured by the falciform process.

The condition of the pterygoid bone can best be interpreted by regarding it in relation to that found in *Platanista* and *Stenodelphis*. In *Inia* the whole of the lateral and superior laminae of the pterygoid has disappeared so that the great wing of the alisphenoid (ALS), which in the other two genera was hidden by the pterygoid, is completely exposed. In the posterior narial region the pterygoid is reduced so that only the mesial lamina (PT (ML)) of the pterygoid hamulus remains, except at the posterior border where fenestrated vestiges of the inferior lamina (PT(IL)) still persist. As a result of the extensive resorption of the mesial lamina, the lateral aspect of the palatine (PAL) is largely exposed, and posteriorly to the palatine a wide lacuna gives entrance to the nares. Because of the reduction of the pterygoid bone there is no osseous evidence of its extension into the orbital region as in *Stenodelphis* but radiographs (see p. 70) show that the air sacs primarily associated with the pterygoid protrude into the orbital region (see Pl. 22). As in *Stenodelphis* there is a posteriorly projecting, but in this genus much fenestrated, maxillary plate. This plate was considered by Flower (1889) to be a portion of the palatine fused anteriorly to the maxilla, but the lateral suture between the palatine and the maxillary plate is situated in the deep fossa formed between the aforementioned plate and the palatine. It should be noted that in the post-orbital region of the majority of the specimens of *Inia* examined, the maxillary is exposed to view on its ventral aspect owing to resorption of the frontal (FR).

The greater wing of the sphenoid, part of the parietal and the greater part of the ventral aspect of the frontal present a smooth, polished appearance. It will be demonstrated later that this smoothness is associated with the proximity of the bones to air sacs.

The tympano-squamosal recess (TSQR) is much shallower than in the other two River Dolphins. The anterior angle extends as far as the border of the squamo-cranial notch but does not extend along the mesial margin of the zygomatic process (SQZ) as in *Stenodelphis*. The borders of the recess are not strongly involuted as in the other two genera.

In the only available specimen of *Lipotes* (Pl. 23) the tympano-periotic bones are *in situ* so that the hiatus and the recesses in the paroccipital process cannot be seen, but the general impression which is possible suggests considerable separation of the tympano-periotic bones from the adjacent bones of the skull.

The falciform process has completely disappeared as has also the bony infundibulum of the foramen ovale (FO.) The foramen ovale in this species appears to form a discrete perforation of the alisphenoid but is in fact a re-entrant of that bone, the distal borders being in close apposition in a manner comparable with the condition found in *Physeter* and *Kogia*.

The basioccipital crests (BOC) are more prominent than in *Inia*, but as in the latter are rather thin and plate-like.

The condition of the pterygoids is similar to that in *Inia* but the hamuli (PTH) do not project posteriorly to the same extent as in that species. On the other hand the postero-lateral borders of the pterygoids extend ventrally beyond those of the basioccipital crests so that a deep notch is formed in the crest at the point of junction of the two bones. The lateral lamina is almost as completely resorbed as in *Inia* and the mesial lamina (PT(ML)) is absent anterior to its junction with the posterior edge of the palatine (PAL.) There is no trace of the superior or lateral lamina in the orbital and post-orbital regions and the great wing of the alisphenoid (ALS) is completely exposed. The post-orbital process of the frontal is greatly widened as compared with *Inia* and its ventral surface is smooth as in that genus.

The development of the tympano-squamosal recess (TSQR) shows a considerable advance on *Inia*, its anterior process projecting halfway along the mesial border of the zygomatic process of the squamosal (SQ).

MONODONTOIDEA

Except in the lesser prominence of the falciform process *Monodon monoceros* shows a less advanced state of resorption of the bones associated with the air sinuses than *Delphinapterus* and therefore will be dealt with first.

In the figure of the skull of an adult *Monodon* (Pl. 13) it will be seen that the tympano-periotic bones are missing, but the figure of that of a very young specimen (Pl. 14) shows the position which they occupy and how their ventral surfaces are level with the basioccipital crest (BOC). It will be noted that the mastoid process (MAS) is completely dissociated from the adjacent bones of the skull. In the juvenile specimen there is a wide hiatus in the cranial cavity above the tympano-periotic bone but in the adult (Pl. 13) this has been largely filled in by extensions from the squamosal, parietal and alisphenoid.

The falciform process (FP) is a low, rather stout tubercle (Pl. 13). Of the bony tube of the foramen ovale (FO) which transmits the mandibular branch of the trigeminal nerve the anterior, dorsal and ventral walls of its mesial portion remain, *Monodon* in this respect being unlike *Inia* in which only a very small, spike-like portion of the wall persists (see p. 46 *supra*).

The basioccipital crests are more prominent and the laryngeal arcade between them more heightened than in the River Dolphins. The crests themselves are stouter and show a condition of excavation of their lateral aspect similar to that of *Stenodelphis*. The excavation of the paroccipital process (PAO) consists of a saucer-like depression with an anterior communication into the peribullary space ; there is no evidence of a ventral closing wall as in *Platanista*.

The space between the mesial (PT (ML)) and lateral laminae (PT (LL)) of the pterygoid, which involves palatine and alisphenoid bones, is considerably more distended than in any of the River Dolphins. Posteriorly the superior lamina (PT (SL)) of the pterygoid has disappeared exposing to view most of the greater wing of the alisphenoid, as in *Inia*. In this respect the posterior region of the pterygoid shows a more advanced state of resorption than that of the anterior region. The pterygoid hamuli (PTH) are only slightly excavated and their mesial borders are widely separated anteriorly and approximately but not touching posteriorly.

The lateral laminae of the alisphenoid, pterygoid and palatine on each side, form a bony bridge extending posteriorly from the anterior border of the orbital process of the frontal to the squamosal. The greater part of the ventral portions of these laminae has disappeared leaving a wide, gaping, irregular concavity on the ventrolateral aspect of the skull.

The overgrowth of the palatines by the pterygoids is less conspicuous than in the River Dolphins, large areas of the palatine bones being visible on the ventral aspect of the skull.

The tympano-squamosal recess (TSQR) is wide by comparison with that of any of the River Dolphins. Its anterior border is ill-defined, its mesial and lateral borders slightly involuted.

In the figured specimen (Pl. 15) of the skull of *Delphinapterus leucas* the tympano-periotic bone is wanting, showing the dissociation of these bones from the adjacent bones of the skull. The cranial hiatus (CRH) is seen in the figure as are the osteosclerotic extensions of the basioccipital (BO), parietal (PAR), alisphenoid (ALS) and squamosal (SQ). An examination of a number of skulls of adult specimens shows that the hiatus eventually becomes almost entirely obliterated by such extensions.

The falciform process (FP) is much more prominent in this species than in *Delphinapterus* and bears, on its mesial surface proximally, a residual part of the wall of the bony tube of the foramen ovale. Remnants of the mesial part of this tube are also found in the same relative position and in the same form as in *Monodon*.

The basioccipital crests (BOC) are robust and prominent. The paroccipital excavations like those of *Monodon* are open ventrally to expose a shallow depression communicating anteriorly with the peribullary space.

As in *Mondon*, the posterior portion of the superior lamina (PT (SL)) of the pterygoid has disappeared exposing a part of the alisphenoid (ALS) ; the state of development of the anterior portion is also very similar to the condition found in *Monodon*, there being no lateral extension of the pterygoid inter-laminar space in the orbital region. The pterygoid hamuli (PTH) are more excavated and the juvenile specimen figured shows considerable fenestration of their ventral surfaces.

Of the bony bridge, which in *Monodon* extends posteriorly from the anterior border of the supra-orbital process of the frontal to the squamosal, very little remains. The alisphenoidal portion of this lateral lamina is wanting. The pterygoid portion (PT (LL)) is fragmentary and irregularly bordered, with a slender extension posteriorly to the squamosal. Its anterior border is separated from the lateral lamina of the palatine (PAL (LL)) by a short gap. The lateral concavities in the ventral aspect of the skull are thus still delineated mesially by the basioccipital ridges and laterally by the above-mentioned bony bridges. It should be noted that the anterior end of the concavities excavate the palatine bones to a greater extent than in *Monodon*. The pterygoids do not override the palatines anteriorly but make deep invaginations into the posterior borders of the latter. The hamuli are similar to those of *Monodon*, being separated mesially from each other, their mesial borders being wider apart anteriorly than posteriorly.

As in *Mondon* the tympano-squamosal recess is shallow and ill-defined, with almost no involution of any of the borders.

DELPHINOIDEA

PHOCAENIDAE (Pls. 26, 27, 28). The tympano-periotic in the specimen of *Phocaena phocoena* figured (Pl. 26) is missing, being dissociated from the remainder of the skull. The cranial hiatus (CRH) dorsal to the ear bones is partly filled by osteosclerotic extensions of the basioccipital (BO) and parietal (PAR).

The falciform process (FP) is reduced to a low, rounded, ventro-mesially projecting, thin blade. Of the bony tube of the foramen ovale (FO) only a minute fragment of the mesial portion remains and the foramen itself is very much enlarged.

The basioccipital crests (BOC) are very prominent but very thin, being fenestrated in the region mesial to the peribullary space. Posteriorly and mesially to the tympanic bulla the edge of the crest is strongly involuted so that it forms a partial floor to the peribullàry space. The paroccipital processes are deeply excavated on the anterior face and bear a shallow depression on their antero-ventral aspect.

The whole of the superior lamina of the pterygoid has disappeared so that the wing of the alisphenoid (ALS) and the ventral face of the orbito-sphenoid (OS) are exposed. The mesial lamina (PT(ML)) and the sphenoid wing form a deep, trough-like fossa anterior to the peribullary space. The lateral lamina of the pterygoid (PT (LL)) remains as a narrow, perforated, irregularly-edged strip of bone connected anteriorly to the palatine and posteriorly to the alisphenoid (Pl. 26).

Although no bony remnants of an orbital distention of the pterygoid bone remain, it is known that an extension of the air sinus system passes dorsally and posteriorly into a deep cavity, the walls of which are formed by the anterior face of the frontal and the ventral face of the maxillary bones (MX). A great part of the mesial wall of this cavity is formed by a portion of the mesial lamina of the pterygoid.

The pterygoid hamuli (PTH) are more extensively excavated than in the Monodontidae and are frequently fenestrated on their ventral surface. The hamuli are widely separated, with their mesial borders divergent caudally.

The tympano-squamosal recess is extended laterally in front of the glenoid fossa. Its lateral border is involuted.

The arrangement of the bones under discussion in *Neomeris phocaenoides* (Pl. 28) is essentially as in *Phocaena phocoena* with, however, some noteworthy differences. The basioccipital crests (BOC) are more robust but not so strongly involuted in the region of the tympanic bulla. The fossae formed by the mesial lamina of the pterygoid (PT (ML)) and the greater wing of the sphenoid, and that on the anterior face of the cranium, are enlarged. The bony bridge formed by the lateral lamina of the alisphenoid, which is reduced to a minute promontory, extends anteriorly to the postero-dorsal angle of the pterygoid bone.

DELPHINIDAE (Pls. 29–35). *Pseudorca crassidens*, so far as the region of the skull under consideration is concerned, shows the most primitive arrangement existing in any of the Delphinidae. In the plates (Pls. 29, 30) the tympano-periotic is missing so that the great extent to which the cranial hiatus has been obliterated by secondary osteosclerosis is well-demonstrated; only the foramina for the transmission of blood vessels and nerves persist.

The falciform process (FP) is a broad, irregularly-outlined, robust plate the posterior margin of which, proximally, follows the contour of the tympanic bulla situated immediately behind it. The bony tube which transmits the mandibular branch of the fifth nerve is represented by spicular, bony elements involving the pterygoid and alisphenoid. They extend from the cranial wall obliquely and caudally to make contact with the inner aspect of the falciform process.

The basioccipital crests (BOC) are very stout and extensively cavitated on their lateral aspect. They are not very prominent so that the laryngeal arcade is correspondingly shallow as compared with that of other Delphinids. The depressions on the ventral aspect of the paroccipital processes (PAO) are rather ill-defined.

Pseudorca crassidens shares with *Balaenoptera musculus* the distinction from other forms of having the falciform process in contact with the posterior border of the palatine. Thus there is a continuous bony bridge, as in certain species previously described, but it is deficient in bony elements of the pterygoid and alisphenoid, the lateral bony lamina consisting solely of extensions of the palatine (PAL (LL)) and squamosal (SQ). A considerable portion of the superior lamina of the pterygoid (PT(SL)) is still present but it does not cover the alisphenoid to any great extent. Laterally the ventral border of the mesial lamina of the pterygoid (PT(ML)) is deeply excavated by numerous, and for the most part longitudinally-directed, indentations which continue for a distance into the posterior nares. At their terminus there originates a posteriorly directed bony groove which lies along the mesial aspect of the ventral border of the pterygoid. As in the River Dolphins, notably *Stenodelphis*, there is an extension of the pterygoid above the plate of the palatine which has a distinct horizontal, laterally-directed flexure in this area. This orbital extension is much better defined and more strongly developed than that of the River Dolphins, and, owing to the presence of a large optic nerve, is divided into two distinct lobes, the one passing round the anterior margin of the optic foramen, the other posterior to the foramen. In the amount of osseous content remaining in the prepared skull there is considerable individual variation within the species. In the specimen shown in Plate 29, the inferior, mesial and lateral laminae of the orbital extension of the pterygoid are complete, so that the inter-laminar space is enclosed in an unperforated bony case, whereas in the specimen shown in Pl. 30, the bony laminae are so rarified that only a cage-like remnant persists.

On the palatal surface the palatine bones (PAL) are widely exposed, but their posterior face is deeply invaginated by the forward extension of the cavity of the pterygoid hamuli (PTH). The hamuli are strongly excavated and their mesial borders are in close apposition in the middle line.

The tympano-squamosal recess (TSQR) is wide, shallow and ill-defined, but its anterior extension reaches almost to the anterior tip of the zygomatic process.

The tympano-periotic bones are absent in the specimen of *Orcinus orca* figured (Pl. 31). The cranial hiatus (CRH) shows dimensions consonant with the juvenile condition of the skull, there being little osteosclerosis of the marginal bones.

The falciform process (FP) is more attenuated than in *Pseudorca*, being a sickle-shaped, narrow plate with irregularly pointed extremity. The bony tube of the foramen ovale (FO) is represented by a small flange projecting from the cranial wall. On the mesial face of the falciform process there is a small tuberosity which apparently represents the last vestige of the distal end of the tube.

The basioccipital crests are moderately thin and prominent, with a small amount of cavitation of their lateral aspect. The depressions of the paroccipital processes (PAO) like those of *Pseudorca* are rather ill-defined.

The lateral lamina and the greater part of the superior lamina of the pterygoid bone, except in the hamular region, have disappeared. A large area of the alisphenoid (ALS) is exposed. A small portion of the superior lamina (PT (SL)) persists, covering the mesial end of the ventral face of the orbito-sphenoid and a small part of the adjacent alisphenoid. The mesial lamina (PT (ML)), as in *Pseudorca*, is scored by a number of longitudinal grooves on the ventral margin; they are not however, as conspicuous as in *Pseudorca crassidens*. As in *Pseudorca* there is an extension of the pterygoid (PT) into the pre-orbital region although it is more resorbed than in that species. It extends anteriorly from the mesial lamina of the pterygoid as a small, recurved, finely fenestrated plate of bone which lies alongside the lateral face of the palatine. A feature, which is distinctive of *Orcinus*, is that the fossa which gives access to the maxillary foramen is very much enlarged relative to that of other dolphins. It is confluent with the pre-orbital smoothed area. Parts of the jugal and maxilla lateral to the pre-orbital smoothed area have a flattened squamous appearance above the position of the eye. In the position occupied by the post-orbital extension of the pterygoid in *Pseudorca* there is in *Orca* a shallow depression on the ventral surface of the frontal, in which the bone is of a smoother texture than that which surrounds it. The smooth area in the preorbital region is considerably larger than the area occupied by the preorbital extension of the pterygoid in *Pseudorca*. The significance of these features is referred to on p. 96.

The pterygoid hamuli (PTH) are moderately excavated, their ventral aspects being fenestrated (this latter condition is usually associated with juvenile specimens) and their mesial borders are in contact in the middle line. The palatine bones (PAL) are extensively exposed ventrally and laterally and their posterior faces are very strongly invaginated.

The tympano-squamosal recess is wide and well defined; its anterior extremity extends about halfway along the mesial border of the zygomatic process of the squamosal. The antero-mesial margin is involuted.

In the specimen of *Orcaella* figured (Pl. 32) the tympanic bulla and periotic are absent and the infilling of the cranial hiatus (CRH) is composed of an osteosclerotic extension of the parietal.

The falciform process (FP) is slender, curved and ventrally projecting. A very small laterally-projecting spine on the ventral margin of the foramen ovale (FO) represents the last remnant of the bony tube of the fifth nerve mandibular branch.

The basioccipital crests (BOC) are thinner than those of *Orcinus*. The paroccipital processes (PAO) are marked by shallow excavations of the anterior face.

Posteriorly not a vestige remains either of the superior or of the lateral lamina of the pterygoid, nor is there a trace of the lateral lamina of the alisphenoid. The greater wing of the sphenoid (ALS) and most of the orbito-sphenoid (OS) are exposed, and a large hiatus is present in the region of the optic canal (OF). There is a small remnant of the orbital extension of the pterygoid in the form of a narrow shelf (PT(SL)) and a slender, curved spine extending laterally from the mesial lamina of the pterygoid (PT (ML)) along the anterior border of the orbito-sphenoid. In this position the palatine bone shows a conspicuous, horizontal, laterally-directed flexure (PAL (LL)). As in *Orcinus* there are two smoothed depressions in the ventral surface of the frontal corresponding in position to the pre- and post-orbital extensions of the pterygoid noted in *Pseudorca*. The anterior depression is much larger than the posterior and communicates with a cavity which lies between the frontal and maxillary bones on the front of the cranium. There is also a small, smoothed area on the proximal end of the maxilla. In the relative extent of the smoothed areas *Orcaella* resembles *Orcinus*.

The pterygoid hamuli (PTH) are excavated but not inflated and their mesial borders are widely separated.

In *Orcaella* the anterior prolongation of the tympano-squamosal recess (TSQR) extends almost to the anterior limit of the zygomatic process of the squamosal.

In the *Globicephala melaena* skull figured (Pl. 33) the tympano-periotic bones are lacking. The cranial hiatus (CRH) is very largely occluded so that only the foramina of the nerves remain. The falciform process (FP) is a truncated, irregular plate, which bears no trace of the bony tube of the foramen ovale (FO) on its mesial aspect. A small flange on the alisphenoid (ALS) represents the proximal end of this tube.

The basioccipital crests (BOC) are moderately stout and shallowly cavitated on their lateral aspect.

The depressions on the paroccipital processes (PAO) are separated only by a very low ridge from the peribullary space.

The lateral lamina of the pterygoid is completely wanting, but a small remnant of the lateral lamina of the alisphenoid remains in the form of a low, ventrally projecting ridge at the lateral extremity. Of the superior lamina of the pterygoid the greater part of the posterior portion is wanting, exposing the wing of the alisphenoid (ALS). Anteriorly however there is a fairly wide plate of the lamina (PT (SL)) underlying the orbitosphenoid (OS). No bony vestige remains of the pre-orbital extension of the pterygoid, but the whole of this region is deeply recessed and is partially lined by a squamous extension of the palatine bone (PAL), the remainder of the recess involving the maxilla (MX). An extension of the recess passes dorsally and posteriorly, between the frontal and the maxilla. The two smoothed depressions on the ventral aspect of the frontal bones which were observed in *Orcinus* and *Orcaella* are also present in *Globicephala* but there is an enlargement of the posterior depression corresponding with the enlargement of the anterior one, so that both are equal in area. To this extent *Globicephala* differs from the other two genera just mentioned, in which the posterior depression is relatively insignificant.

The pterygoid hamuli (PTH) are entirely excavated and very widely dilated, and in juvenile specimens there is fenestration of the ventral aspect. The mesial borders of the two hamuli are in contact. Anteriorly the palatine bones are not extensively overgrown by the pterygoids and the invagination of their posterior face is only moderate.

The tympano-squamosal recess (TSQR) extends to the anterior tip of the zygomatic process of the squamosal, as in *Orcinus*.

The tympano-periotic bones are dissociated from the skull of the specimen of *Feresa intermedia* figured (Pl. 35) and the cranial hiatus (CRH) is partially obliterated by extensions from the bones adjacent to it. The margins of the peribullary sinus are deeply involuted, particularly in the anterior region. Here the wing of the sphenoid is divided horizontally into two laminae by an extension of the peribullary space.

The falciform process (FP) is broken but the remaining basal part suggests that it consisted of a small hamate plate of bone. The fracture is such that it is impossible to state whether any remnant of the distal end of the bony tube of the foramen ovale remains. The proximal end of the tube is well-defined.

The basioccipital crests (BOC) are slender but quite prominent, and involuted laterally on their ventral margin. The depression in the paroccipital process (PAO) is moderately defined.

No vestige of the lateral and superior laminae of the pterygoid bone remains except for a small shelf of the superior lamina (PT (SL)) below the orbitosphenoid (OS). In both the specimens available there is secondary cavitation of the alisphenoid (ALS) and frontal (FR). Of the pre-orbital extension of the pterygoid only part of the mesial lamina remains and the pre-orbital region generally is recessed as in *Globicephala melaena*, the recess being partially lined by a squamous extension of the palatine bone. The recess between the frontal and maxillary is moderately well developed on the right side but not so evident on the left. The two pre-orbital recesses of each side are markedly asymmetrical, that on the right being much larger than the other. The smoothed, post-orbital recesses are larger in area in relation to the preorbital than in *Globicephala*.

The pterygoid hamuli (PTH) are widely dilated, and they are extensively fenestrated on their ventral aspect. As their posterior extremities are missing it is impossible to state whether the pterygoids meet in the middle line, but it seems likely that they do. The palatine bones (PAL) are not extensively overgrown by the pterygoids but their posterior faces, as well as those of the maxillae, are deeply invaginated by an intercalation of the pterygoid cavity.

The tympano-squamosal recess (TSQR) is relatively extensive, its anterior extremity spreading out and occupying the whole of the ventral surface of the anterior apophysis of the zygomatic process of the squamosal.

Cephalorhynchus heavisidei and *C. commersoni* are sufficiently alike to be considered together. In the figured specimen of *C. heavisidei* (Pl. 36) the tympano-periotic bone is dissociated from the skull so that the very large cranial hiatus (CRH) is exposed. The falciform process (FP) is a wide, bifurcated bone with no trace of the infundibulum of the mandibular branch of the 5th nerve on its mesial aspect. A short length of the mesial portion of the infundibulum protrudes from the wing of the sphenoid bone partially surrounding the foramen ovale (FO).

The basioccipital crests (BOC) are thin, partially excavated and moderately involuted. There is a small recess on the ventral face of each of the paroccipital processes (PAO). The pterygoid plate and hamuli are wanting but from observation of a complete specimen of *C. commersoni* no trace of the superior or lateral laminae of the pterygoid remains.

The bony orbital extensions of the pterygoid are absent and a very deep pre-orbital recess passes between frontal and maxilla. The post-orbital recess on the ventral aspect of the frontal is almost contiguous with the pre-orbital recess and has a posteriorly projecting extension under the post-orbital processs of the frontal (FR (PO)). In this respect, and in the degree of excavation of the pterygoid hamuli, together with the separation of the hamuli, *Cephalorhynchus* compares with *Phocaena*.

The tympano-squamosal recess (TSQR) is limited in area, extending only halfway along the mesial border of the zygomatic process of the squamosal—another respect in which it bears some resemblance to *Phocaena*.

The skull of *Lagenorhynchus albirostris* examined but not figured, lacks the tympano-periotic bone and, as in *Pseudorca crassidens*, the cranial hiatus is filled by secondary bone except for the foramina. The falciform process is a wide, irregularly-shaped, thin plate with a slender, ventrally directed spine which makes contact with the anterior extremity of the bulla. The remnants of the bony tube of the foramen ovale consist of a few postero-laterally directed spicules as in *Pseudorca crassidens*.

The basioccipital crests are thin, plate-like, very prominent ridges. The depressions of the paroccipital processes are shallow.

In Pl. 37 which shows the anterior portion of a cranium, the bony bridge of the lateral lamina consists of elements of the alisphenoid (ALS), pterygoid (PT (LL)) and palatine (PAL (LL)). The pterygoid element, which is much fenestrated, is sutured anteriorly to the lateral corner of the hamular part of the same bone (PTH), in addition to being in contact with the palatine. Although there is no contact between the lateral pterygoid element, and either the superior (PT (SL)) or mesial portions (PT (ML)), its identity as part of the pterygoid bone can be deduced by reference to the condition of the lateral lamina in *Monodon*, in which the lateral portion is joined to the superior portion by small, extremely thin, bony connections. As in previously described species there is, in *Lagenorhynchus albirostris*, an extension of the pterygoid bone into the orbital and pre-orbital regions, but the greater part of its lateral lamina has disappeared. Of the superior lamina of the pterygoid, only that part which underlies the orbito-sphenoid remains.

The pre- and post-orbital depressions on the ventral surface of the frontal are relatively smaller than in *Cephalorhynchus*. *L. albirostris* compares with that genus in having an extension of the post-orbital depression passing posteriorly under the post-orbital process of the frontal.

The pterygoid hamuli are deeply excavated, and elongated, each showing a sharp keel ventrally, a feature which characterizes most of the specialized delphinids. The mesial borders of the hamuli meet in the middle line.

The tympano-squamosal recess (TSQR) is a deep, crescent-shaped fossa bordering the postero-mesial margin of the glenoid fossa. Its anterior extension reaches to about half way along the anterior border of the zygomatic process. The lateral margin is strongly involuted.

Before proceeding with a description of the ventral region of the skull of *Lagenorhynchus acutus*, it should be noted here that the precedence of order in the descriptions has been decided by the extent to which the lateral lamina is evident. The presence or absence of this bony bridge in the prepared specimens is dependent upon the degree of attachment of the bridge elements to the squamosal and palatine. The absence of the component bridge elements does not imply that such elements do not exist, and indeed it has been observed that small fragments of the bridge are sometimes present in the fibrous connective tissue and are usually lost in the process of maceration. The presence of such unconnected ossicles is an indication of greater specialization in the evolution of the air sinuses than is the case when a connected bony bridge persists.

In the figured skull of *L. acutus* (Pl. 39) the tympano-periotic bones are absent, and the partial obliteration of the cranial hiatus (CRH) is illustrated. In this species the cavity occupied by the peribullary sinus is well defined and its borders involuted. The greater extent of this involution, as compared with that present in this region in *L. albirostris*, indicates that, as far as the evolution of the peribullary space is concerned *L. acutus* is in an earlier phase than *L. albirostris*.

The falciform process (FP) is a robust, digitiform plate making contact on its inner face with the bony tube of the foramen ovale (FO). The bony tube is nearly entire in this species and is a conspicuous lateral projection of the cranial wall.

The basioccipital crests are thin, prominent and involuted. The ventral depressions of the paroccipital processes (PAO) are very shallow but the processes themselves are deeply cavitated dorsally, the cavities being confluent with those of the peribullary spaces.

Whether or not any portions of the bony bridge of the lateral lamina are present in the living animal has not been ascertained but the state of resorption of the superior lamina indicates that if such remnants are present they will be very small. The superior lamina is restricted to a narrow strip bordering the mesial margin of the orbito-sphenoid (OS). The alisphenoid (ALS) is completely exposed. The extension of the pterygoid bone into the pre-orbital region is strongly reminiscent of the condition found in the specimen of *Pseudorca* shown in Pl. 30. It consists, on the right side, of a pointed, laterally projecting loop of bone (see Pl. 39) on the left side it forms a small, flat, oblique, fenestrated projection. There is a slight lateral flexure of the palatine bone (PAL (LL)) adjacent to it.

The pterygoid hamuli (PTH) are completely excavated and their mesial margins meet in the middle line. The excavation of the hamuli anteriorly does not produce a corresponding invagination of the posterior wall of the palatines as in some species already described. On the palatal surface of the skull the palatine bones (PAL) are exposed to a moderately conspicuous extent.

The pre- and post-orbital smoothed areas on the ventral surface of the frontal are like those of *L. albirostris*.

The tympano-squamosal recess (TSQR) is small and its margins strongly involuted like those of the peribullary space. Its anterior limit extends only a short distance along the anterior margin of the zygomatic process.

In the *Lagenorhynchus obscurus* specimen figured (Pl. 40) the tympano-periotic bones are missing and the cranial hiatus (CRH) is wide and conspicuous, although its original extent is reduced by secondary growth of bone from the alisphenoid and parietal. As in the previous species, there is involution of the border of the peribullary space but not to the same extent.

The falciform process (FP) is a small, roughly triangular plate. Of the bony tube of the foramen ovale (FO) only a small portion of its cranial end remains.

The basioccipital crests (BOC) are extremely thin and delicate. The depressions on the paroccipital processes (PAO) are more conspicuous than in *L. acutus*, and there is a slight excavation of the anterior face of the processes themselves.

No part of the lateral lamina of the pterygoid and alisphenoid remains, and of the superior lamina (PT (SL)) only a small plate extends under the orbito-sphenoid. On the right side, this plate has a small, lateral, strap-like projection (see Pl. 40 (PT)). Of the orbito-pre-orbital bony extension of the pterygoid, only a minute, anteriorly projecting spicule remains, but the pre-orbital regions of the lateral face of the palatine and maxillary are strongly recessed, the bone in this area being of the characteristic smoothness associated with proximity to air sacs.

The pre-orbital depressions on the ventral face of the frontal are conspicuously larger than those of *L. albirostris* or *L. acutus*, and give indication of coalescence with the post-orbital smoothed areas. The latter are comparable in extent to those of the species just mentioned.

The pterygoid hamuli (PTH) are completely excavated, their mesial borders being parallel proximally but strongly divergent distally. The excavation of the hamuli does not involve invagination of the posterior face of the palatines (PAL), and the latter are themselves moderately conspicuous on the palatal aspect of the skull.

The tympano-squamosal recess (TSQR) on each side is conspicuous, its margin involuted, the anterior extremity extending as far as the anterior end of the zygomatic process of the squamosal. This extension is obscured in Pl. 40 by the glenoid fossa.

In the figured skull (Pl. 41) of *Grampus griseus* the tympano-periotic bones are missing and the cranial hiatus is obliterated by secondary bone, except for the foramina of the auditory nerve and the foramen lacerum posterius.

The falciform process (FP) is narrow and irregularly outlined. On its mesial face it bears a small shelf of bone which sutures with the distal end of the bony tube of the foramen ovale, thus the ventral wall of this tube is complete. Between the mesial face of the falciform process and the lateral edge of the bony tube of the foramen ovale (i.e. alisphenoid) a small, irregularly triangular piece of bone is inserted. This is the last vestige of the lateral lamina of the pterygoid bone in this region.

The basioccipital crests (BOC) are moderately stout and not cavitated.

The depressions on the paroccipital processes (PAO) merge anteriorly with the peribullary space.

Apart from the portion of lateral lamina of the pterygoid bone mentioned above, no other trace remains. Of the superior lamina (PT (SL)) the part underlying the alisphenoid is wanting, but beneath the orbito-sphenoid (OS) is a wide, plate-like remnant which extends in places beyond the lateral border of the orbito-sphenoid and bears on its anterior border a small, laterally directed process. Of the pre-orbital bony extension of the pterygoid only portions of the mesial lamina remain, but in this region a wide recess excavates deeply into the lateral face of the palatine (PAL) bone and passes postero-dorsally above the pre-orbital margin of the frontal in a manner similar to that found in *Phocaena phocoena*.

The pre- and post-orbital smoothed areas on the ventral surface of the frontal

(FR) are very extensive and indicate coalescence with one another. The post-orbital extension is widely spread on the postero-ventral face of the frontal. The pre-orbital area extends anteriorly onto the posterior end of the ventral face of the maxilla.

The pterygoid hamuli (PTH) are deeply excavated and dilated, with their ventral aspect frequently considerably fenestrated. In the specimen figured, the palatine bone, on the palatal surface, is partially obscured by the overgrowth of the pterygoid bone, but in the range of specimens available for inspection there is considerable variation in the extent to which the palatine on each side is overgrown by the pterygoid bone. The anterior face of the palatine is deeply invaginated by the forward extension of the cavity of the pterygoid hamulus. The mesial borders of the hamuli meet in the middle line.

The tympano-squamosal recesses (TSQR) are extensive but ill-defined anteriorly.

In the figured specimen of *Tursiops truncatus* the tympano-periotic bones are missing. Pl. 43 shows the cranial hiatus (CRH) largely occluded by secondary bone so that only the well-defined foramina of the appropriate nerves persist.

The falciform process (FP) is of the shape implied by the name given to this portion of the squamosal. No remnants remain of the distal end of the bony tube of the foramen ovale (FO), but a small tuberosity on the alisphenoid (ALS) representing the vestige of this tube is sometimes present proximally.

The basioccipital crests (BOC) are moderately prominent and robust, the posterior portions being slightly involuted. The paroccipital processes (PAO) are excavated anteriorly and ventrally.

The whole of the lateral lamina and the greater part of the superior lamina of the pterygoid have disappeared so that the wing of the alisphenoid (ALS) is widely exposed. Anteriorly a very small remnant of the superior lamina (PT (SL)) overlaps the orbito-sphenoid (OS). The orbito-preorbital extension of the pterygoid bone is represented only by a small portion of the mesial lamina. A small lateral flexure of the palatine (PAL (LL)) in the preorbital region is shown in Pl. 43.

The pre- and post-orbital smoothed areas are very similar to those of *Grampus griseus*, thus there is evidence of coalescence of the two areas lateral to the optic foramen (OF), and of an extension of the post-orbital area onto the postero-ventral face of the frontal (FR (PO)). *Tursiops* differs from *Grampus* in that the pre-orbital extension of the smoothed area on the posterior end of the ventral surface of the maxilla (MX) is longer and much more conspicuous.

The pterygoid hamuli (PTH) are completely excavated but the inter-laminar space is very restricted by the close approximation of the laminae. The ventral surfaces of the lateral laminae are flattened but strongly keeled, their mesial borders meeting in the middle line.

The palatine bones (PAL) are extensively exposed anteriorly and laterally to the pterygoid hamuli and there is little or no excavation of their posterior face by extensions of the hamular cavities.

The tympano-squamosal recess (TSQR) is well-defined; mesially the boundary is involuted, while the forward extension ends little more than half way along the zygomatic process.

The specimen of *Stenella euphrosyne* figured (Pl. 45) shows the tympano-periotic bones (TB) glued approximately in their natural position. It will be seen that the peribullary space separates the ear-bones from the basioccipital crest (BOC) and the paroccipital process (PAO). The ear bones have been glued by the " mastoid process " to the exoccipital bones (EXO) giving an appearance of contiguity with these which is artificial. In the natural state the process is separated from the adjacent bones by a fibrous ligament.

The falciform process (FP) is long and slender and its close relation to the tympanic bulla is well shown in the figure. Of the bony tube of the foramen ovale (FO) only a small vestige of the proximal part remains.

The basioccipital crests (BOC) are very slender and laminate and the paroccipitals (PAO) much reduced in thickness, being deeply excavated on their anterior faces.

The lateral and superior laminae of the pterygoid bones have almost entirely disappeared exposing considerable areas of the alisphenoid (ALS) and orbito-sphenoid (OS) bones. A narrow, irregular desquamation of the superior lamina (PT (SL)) occupies the mesial margin of the orbito-sphenoid. Of the pre-orbital extension of the pterygoid only a portion of the mesial lamina is present. A conspicuous upwardly and backwardly projecting recess in this region is bounded by the maxilla (MX) and the frontal (FR).

The distribution of the pre-orbital and post-orbital smoothed areas is very similar to that of *Tursiops truncatus*, but there is in addition a deep fossa lateral to the orbito-sphenoid which excavates the ventral surface of the orbital process of the frontal, producing a stout ridge of bone along the anterior margin of the frontal in this region. The pre-orbital recess is very deeply excavated and as in *Tursiops* there is an anteriorly attenuating fossa on the hinder end of the ventral surface of the maxilla. It may be noted that *Lagenorhynchus obscurus* shows the above mentioned features although less conspicuously.

The pterygoid hamuli (PTH) are completely excavated and slightly dilated ; their ventral laminae is of a transluscent thinness. The internal walls of the hamular space are reinforced by trabeculae. The palatal aspect of each hamulus is bluntly keeled and the two hamuli approximate closely to each other in the middle line.

The palatal bones (PAL) are extensively exposed anteriorly and laterally to the pterygoid, but are deeply invaginated on their posterior faces by forward extension of the pterygoid cavities.

The tympano-squamosal recess (TSQR) is clearly delineated, its margin being for the most part strongly involuted.

In the adult skull of *Delphinus delphis*, examined but not figured, the tympano-periotic bones were missing and the cranial hiatus was partially occluded by secondary extensions of adjacent bones. The falciform process was comparable with that of *Stenella euphrosyne* and, as in the latter species, there was only a small remnant of the proximal end of the bony tube of the foramen ovale. The basioccipital crests were slender, laminate and very similar to those of *Stenella euphrosyne*.

The paroccipital processes were stouter and not so strongly excavated on their anterior face as in the latter species. They showed the characteristic depression on the ventral face which has been noted in some of the previously described species.

The lateral and superior laminae of the pterygoid had entirely disappeared, and, in the preorbital region, only the mesial lamina remained. In the distribution of the pre-orbital and post-orbital smoothed areas *Delphinus delphis* differs from *Stenella*, only in the maxillary region. Here, a conspicuous, deep, elongated fossa extends on the ventral aspect of the maxilla, diminishing in depth towards its termination near the anterior extremity of the rostrum.

The confluent aperture of the optic foramen, foramen rotundum and sphenoidal fissure was very much enlarged by resorption of the boundary margins of the orbito-sphenoid and alisphenoid.

The pterygoid hamuli were completely excavated and trabeculated as in *Stenella euphrosyne*. The posterior margins of the lateral laminae were extensively resorbed and the keeled ventral surfaces were fenestrated. The hamuli were in close apposition to each other in the middle line.

The juvenile specimen figured (Pl. 46) is in the main similar to the adult but with the following differences. There is a small remnant of the superior lamina of the pterygoid (PT (SL)) covering the mesial part of the orbito-sphenoid (OS). Of the orbital extension of the pterygoid, considerable portions of the superior and mesial laminae remain, and a delicate bridge of bone between these represents the last vestige of the lateral lamina (PT (LL)). Although in this respect the juvenile appears to be more primitive than the adult, the fenestration of the hamular laminae is of much greater extent than in the adult.

The palatine bones (PAL) are extensively exposed anteriorly and laterally to the pterygoid hamuli (PTH), and are quite strongly invaginated on their posterior face by forward extension of the hamular cavities.

The tympano-squamosal recesses (TSQR) are sharply defined but their borders are not strongly involuted as in *Stenella*.

STENIDAE. In the figured specimen (Pl. 24) of *Steno bredanensis* the tympano-periotic bones are wanting and the widely open cranial hiatus (CRH) is plainly visible. The falciform process (FP) forms a broad, spatulate extension of the squamosal (SQ). It is nearly contiguous with cancellated remnants of the bony tube of the foramen ovale (FO).

The basioccipital crests (BOC) are prominent, although slender and plate-like, and the paroccipital processes (PAO) show little excavation of their anterior or ventral faces.

The lateral lamina of the pterygoid bone is wanting except in the hamular region. The superior lamina (PT (SL)) remains as a broad, irregularly bounded plate which partly covers the lateral wing of the alisphenoid (ALS) and posterior portions of the orbitosphenoid (OS).

Of the orbito- pre-orbital extension of the pterygoid, only the mesial lamina remains, but there is a remnant of the lateral flexure of the palatine bone (PAL (LL)) in this region. The pre-orbital and post-orbital smoothed areas indicate coalescence lateral to the optic foramen, with the production of a wide, shallow fossa bounded anteriorly and posteriorly by two smoothed ridges of bone. In comparison with this fossa, the post-orbital extension of the smoothed area below the post-orbital process of the frontal (FR (PO)) is reduced in area. The pre-orbital smoothed area is extended onto the maxilla as in *Tursiops* and *Stenella*.

The pterygoid hamuli (PTH) are deeply excavated, strongly keeled ventrally and their mesial borders meet in the middle line. The palatine bones (PAL) are not extensively covered externally by the pterygoids but their posterior faces are invaginated by forward extension of the pterygoids.

The tympano-squamosal recess (TSQR) is clearly defined, the mesial and anterior margins of the glenoid cavity being slightly involuted. The anterior extension of the recess reaches the anterior limit of the zygomatic process of the squamosal.

The figured specimen of *Sousa plumbea* lacks the tympano-periotic bones (Pl. 25). The cranial hiatus (CRH) is exposed and there is little or no infilling of it by adjacent bones.

The falciform process (FP) is a broad lamina, having a thickening on its mesial aspect with a remnant of the distal end of the bony tube of the foramen ovale (FO). Considerable vestiges of the proximal end of this tube extend laterally from the alisphenoid (ALS).

The basioccipital crests (BOC) are prominent and stout as compared with those of *Steno bredanensis*, their mesial aspect not being excavated to any great extent. The paroccipital processes (PAO) on the other hand are slender, being excavated both anteriorly and ventrally.

The lateral and superior laminae of the pterygoid have entirely disappeared on the left side, but on the right side of the specimen figured a minute vestige of the lateral lamina persists, loosely articulated with the anterior face of the bony tube of the foramen ovale. The lateral aspect of the bony wall of the posterior nares is deeply recessed, the recess being formed dorsally by the ali- and orbito-sphenoid (ALS and OS) and ventrally by a strong involution of the mesial lamina of the pterygoid (PT (ML)).

No trace of the bony orbital extension of the pterygoid remains but there is a very deep recess extending dorsally and posteriorly between the anterior face of the frontal (FR) and the ventral surface of the maxilla (MX). As in *Inia geoffrensis* there is marked resorption of the ventral aspect of the post-orbital process of the frontal so that the maxilla is partially exposed in this region.

Apart from the feature just mentioned the distribution of pre-orbital and post-orbital smoothed areas is comparable with that of *Steno*, *Tursiops* and *Stenella*.

The pterygoid hamuli (PTH) are much fenestrated and a great part of the outer laminae has disappeared. The hamuli are deeply excavated ; numerous trabeculae extend from the inner to the outer lamina between the fenestrations.

The hamuli do not meet in the middle line and their outer surfaces are rounded rather than keeled.

The palatines (PAL) are widely visible and their posterior faces are interpenetrated by trabeculated extensions of the pterygoid hamuli.

The tympano-squamosal recess (TSQR) is very well defined, its margins being involuted both mesially and laterally. Its forward extension terminates some distance short of the anterior end of the zygomatic process of the squamosal.

A skull of *Lissodelphis borealis* became available[1] after the main work contained in this contribution had been completed. Distinctive features of the skull justify inclusion of a description at this late stage.

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[1] By courtesy of Dr. Carl L. Hubbs, Scripps Institution of Oceanography, La Jolla, California.

The tympano-periotic bones are wanting and the cranial hiatus is partially closed. The falciform process is broad basally but extends into a much narrower, irregularly outlined, distal portion. The bony infundibulum of the foramen ovale is of sphenoidal composition only and is prominent.

The basioccipital crests are prominent, slender and plate-like. The paroccipital processes on the other hand are comparatively robust in ventral aspect. The anterior face of each of these processes is excavated by a distinctive cavity with an involuted margin.

The lateral lamina of the pterygoid bone is absent, but the smoothed areas of the skull base as a whole are characterized by their limited lateral extension. Thus the lateral wing of the sphenoid is short, and the smoothed area ends before reaching the spheno-parietal suture. The superior lamina persists as a narrow shelf in the pre-orbital region.

Whilst there is evidence of fusion of the pre- and post-orbital smoothed areas above the optic infundibulum there is practically no extension of the post-orbital lobe under the post-orbital process of the frontal. The pre-orbital smoothed area is extended onto the maxilla as in *Tursiops* and *Stenella*.

The pterygoid hamuli are deeply excavated, strongly keeled ventrally and their mesial borders meet in the middle line. They do not completely cover the palatine bones ventrally.

The tympano-squamosal recess is clearly defined, and the anterior extension of the recess reaches the anterior limit of the zygomatic process of the squamosal.

DISTRIBUTION OF AIR SPACES

The preceding account of the osteological features of the ventral aspect of the cetacean skull was undertaken on the assumption that the form of the various bones and the distribution of smoothed areas was associated with the state of development of the air sinuses connected with the tympanic cavity, and that these sinuses occupied the space between mesial and lateral laminae of bones such as the pterygoid, alisphenoid and palatine.

In most of the skulls examined the greater part of the lateral and superior laminae of these bones was absent, but it has been assumed throughout the account that at some stage in the evolution of the air sinuses the whole of all four laminae (see pp. 33–34) was present. In order to support this hypothesis it was decided to examine the distribution of the air sinuses in detail.

In most cases examination of the distribution of the air spaces involved injection of the latter with a polyester resin, and complete destruction of the soft parts by bacteriological maceration. By this method it was possible to obtain a three dimensional cast of the entire system of air spaces.

ODONTOCETI

In the examination of the River Dolphins the scarcity of material prohibited the destruction of any of the soft parts, so the sinuses of single specimens of *Stenodelphis* and *Inia* were injected with iodized oil and radiographed.

It is unfortunate that no specimen of *Platanista* was available, since this is the only species in which the lateral laminae of pterygoid, alisphenoid and squamosal are complete.

In *Stenodelphis* the greater part of these laminae is present, though much perforated, and it is this species which demonstrates most clearly the close association between the distribution of the air sinuses and the various extensions of the pterygoid bone. In addition, the sinus distribution in *Stenodelphis* provides a guide to the interpretation of sinus formation in species in which no trace of a lateral lamina can be found, and provides strong evidence that such a lamina may have been present at an earlier stage in the evolution of these species.

STENODELPHIS BLAINVILLEI

Pl. 20 is a dorso-ventral radiograph of the head of *Stenodelphis* after injection of the air sinuses with iodized oil. The opaque area shows the distribution of the air space in the horizontal plane and its five main components have been indicated by the names originally applied to the air sacs by Beauregard (*vide supra*). From the point of view of the evolution of these air spaces it is preferable to refer to them as sinuses.

The posterior sinus.

This can be seen as a small, opaque promontory occupying the position of the cavity in the paroccipital process. On the left side the sinus is incompletely filled with the injection medium so that the concavity of the paroccipital process is partly visible as a small, rounded transparent area.

The peribullary sinus

The shadow of the tympanic bulla is completely obliterated by a conspicuous, opaque area in the tympanic region. This opaque area marks the position of the peribullary sinus and demonstrates the extent to which the tympano-periotic bones are surrounded by the sinus. Most of the ventral region of this opaque area is the shadow-graph of that part of the peribullary sinus which lies dorsal to the tympanic bulla separating the latter from the bones of the cranium.

The pterygoid sinus

The name " pterygoid sac " was applied by Beauregard only to that part of the air sinus system which occupies the pterygoid hamuli, the remainder of the system anterior to the tympanic cavity being designated the anterior sinus. As, however, it can be shown that nearly the whole of the anterior air sinus system is associated with the extensions of the pterygoid bone previously described, the authors have found it necessary to include all but the most anterior extremities of the air sinus system in the description of the pterygoid sinus. In the radiograph this sinus is represented by the two conspicuous, wing-like, opaque areas which lie anterior to the tympanic region—as well as by a triangular projection which marks the position of one of the pterygoid hamuli. It will be noted that the opacity extends and partially fills the orbital and pre-orbital parts of the skull—occupying areas normally filled by the optic muscles. In this region there are numerous, irregular, semi-transparent patches. Comparing the distribution of opaque areas with the description and figures of the osteological characters in this area, it will be seen that the pterygoid sinus is almost exactly delineated by the boundaries of the pterygoid bone with all its distentions. The external surface of the sinus is almost completely covered by the thin, lateral lamina of pterygoid bone, although the latter is much perforated, and in the orbital region trabeculated and ruptured by a number of large fenestrations. The small, irregular, semi-transparent patches in the radiograph serve to indicate the cavitation of bone in this region.

Laterally the pterygoid sinus extends as far as the spheno-parietal suture, covering over the greater part of the lateral wing of the alisphenoid.

The anterior sinus

Throughout the descriptions which follow, the name anterior sinus will be applied only to parts of the air sinus system which extend further forward than the most anterior limits of the pterygoid bone. In *Stenodelphis* it is evident that no anterior sinus is present, and that, although the pterygoid lamina is fenestrated in the pre-orbital region, there has been little further extension of the sinus system.

The middle sinus

The radiograph shows a small, triangular, opaque protrusion extending antero-laterally from the general opacity of the peribullary sinus. This protrusion coincides with the position of the tympano-squamosal recess and marks the position of the middle sinus. Its concavity is shown by the semi-transparent streak along its central axis. Although obscured by the peribullary sinus, the point of emergence of this sinus from the tympanic bulla lies immediately dorsal to the tympanic membrane. It was this factor which led Beauregard to homologize it with the " glove finger " of the Mysticeti. This matter is discussed in Part I of Hearing in Cetaceans, Fraser & Purves (1955).

INIA GEOFFRENSIS

Pl. 22 is the dorso-ventral radiograph of the head of *Inia geoffrensis*—the air sinuses of the right side having been injected with iodized oil. The left side is not injected so that the relationship of the air spaces to the various osteological features can be seen.

The posterior sinus

This was the sinus through which the injection was made and its outline is partly obscured by the spillover of the injection medium. It can be seen as a small, reniform, opaque area occupying the position of the paroccipital process, the latter being distinctly outlined on the left side.

The peribullary sinus

The shadow of the tympano-periotic bones is shown on the left side—and from the right side of the radiograph it will be seen that the peribullary sinus completely surrounds this bone. As in the previously described species, the centre of the mass represents the air space between the periotic and the skull and coincides with the position of the cranial hiatus.

The pterygoid sinus

Passing forward from the tympanic region, two narrow, opaque areas can be seen lying along the mesial and lateral aspects of the basi-occipital crest. The mesial opacity demonstrates the form and direction of the Eustachian tube. The tube is widely dilated at its emergence from the tympanic bulla but is compressed mesolaterally as it proceeds forward in the direction of the choanae. The lateral opacity marks the beginning of the pterygoid sinus, and at a short distance forward from the tympanic region it widens laterally to form an irregular, opaque patch covering the area of the wing of the sphenoid bone. Anterior to this patch the opacity increases in dimension and divides eventually into three distinct lobes. The lateral lobe passes forward into the pre-orbital, orbital and post-orbital regions, the last extension continuing dorsally and posteriorly along ventral surface of the post-orbital process of the frontal. The mesial lobe invades the triangular concavity of the pterygoid hamulus.

The anterior sinus

The remaining lobe of the pterygoid sinus extends beyond the orbital and hamular lobes and penetrates the bony rostrum, passing forward inside this part of the skull for a short distance. As this extension is clearly beyond the limits of the bony part of the pterygoid it has been designated the *anterior sinus*.

With the exception of the anterior sinus none of the above-mentioned air spaces is covered laterally by a bony lamina—in this respect differing markedly from the condition found in *Stenodelphis*. Reference to the description of the osteological features on p. 45 shows that the disappearance of the lateral and superior laminae of the pterygoid hamuli, as well as the resorption of the ventral surface of the post-orbital process of the frontal, has occurred in close correlation with the extension and distension of the pterygoid sinus. The continuation of the anterior sinus between the bones of the rostrum is of interest in connection with the condition of this sinus in *Delphinus delphis* (see p. 70).

The middle sinus

The rounded concavity of the tympano-squamosal recess has not been filled with the injection medium, but on the basis of the evidence from *Stenodelphis* and other species hereafter to be described, it is very probable that the recess marks the position of the middle sinus.

PHOCAENA PHOCOENA

The air spaces of the specimen figured on Pl. 27 have been filled with polyester resin and the soft parts removed.

The posterior sinus

A small portion of this sinus can be seen protruding from the posterior aperture of the tympanic bulla. The sinus is not completely filled and would normally occupy the ventral concavity of the paroccipital process. Its normal outline has been indicated on Pl. 27 by a dotted line.

The peribullary sinus

Parts of the peribullary sinus can be seen lying between the tympanic bulla and the basioccipital crests but the greater part is concealed by the tympano-periotic. The latter bone is completely separated from the cranium on its superior aspect by an extension of the peribullary sinus. In the specimen figured, the deep cavity lying anterior to the periotic and postero-ventral to the falciform process is partly filled by a cavernous venous plexus.

The pterygoid sinus

The main mass of the Eustachian tube and the pterygoid sinus can be seen emerging from the anterior aperture of the tympanic bulla. That part which lies along the ventral edge of the mesial lamina of the pterygoid represents the lumen of the Eustachian tube though its outline is not clearly shown. The remaining mass passes forward round the ventral and anterior margins of the foramen ovale, partly covering the alisphenoid and extending into the orbital and pre-orbital regions of the skull and the pterygoid hamuli. On the exterior face of the mass can be seen small fragments of bone which represent respectively the remaining vestiges of the lateral laminae of the pterygoid and alisphenoid. (In *Platanista* these laminae form a continuous sheet of bone reaching from the pterygoid hamulus to the falciform process (see p. 44)). In the post-orbital region a small extension of the pterygoid sinus passes backwards over the alisphenoid, and dorsally and posteriorly under the post-orbital processes of the frontal bones in a manner similar to the condition found in *Inia geoffrensis*. As in the latter species, the surface of the bone is frequently resorbed in this area. Anteriorly the pterygoid sinus passes under the lateral lamina of the palatine bone and invades the pre-orbital concavity, a small lobe of the sinus passing ventrally for a short distance. The pre-orbital part of the pterygoid sinus gives off a diverticulum which passes upwards between the anterior aspect of the frontal and the ventral face of the maxilla.

The anterior sinus

There is no evidence of an extension of the pterygoid sinus beyond the pre-orbital region.

The middle sinus

This sinus has not been completely filled but its proximal position can be seen at its emergence from the aperture above the annulus of the tympanic bulla. The portion of the sinus figured occupies part of the tympano-squamosal recess and in its fully inflated state would occupy the whole of this recess.

LAGENORHYNCHUS ALBIROSTRIS

Pl. 38 shows the cast of the air spaces of left side of a skull of *Lagenorhynchus albirostris.*

The posterior sinus

Only a small portion of the posterior sinus can be seen protruding from the posterior aperture of the tympanic bulla, but the ventral recess on the paroccipital process, into which this sinus protrudes, can be seen in the figure. A dotted line indicates the normal limit of the sinus in its distended state.

The peribullary sinus

The ventral border of the peribullary sinus is visible between the mesial aspect of the tympanic bulla and the lateral aspect of the basioccipital crest. Between the periotic and the falciform process there is a fibro-venous plexus as in *Phocaena.* Close examination of the plexus shows that it contains, between the ramifications of the veins, a reticulate mass of minute, bony trabeculae, the significance of which will be understood when considering the progress of development of the peribullary sinus (see p. 79).

The pterygoid sinus

This sinus emerges from the bulla as a diverticulum of the Eustachian tube, and as the latter has not been injected, its relationship to the sinus has been indicated in Pl. 38. Anterior to the bulla the sinus passes round the ventral margin of the falciform process and the ventral and anterior margins of the foramen ovale. It continues along the lateral aspect of the mesial lamina of the pterygoid and enters the post-orbital, orbital and pre-orbital regions as well as the pterygoid hamuli. In the pterygoid region a considerable vestige of the lateral lamina of the pterygoid bones remains. In the specimen figured the vestige is limited in its backward extension to a point about 1 cm anterior to the falciform process but in most of the specimens examined the bony bridge is more complete although very much fenestrated. Pl. 37 shows the condition of this lamina (PT(LL)) in the majority of individuals examined. It should be noted that the alisphenoid is only partly covered by the sinus.

It has been emphasized that in *Phocaena phocoena* and in this species the posterior part of the pterygoid sinus passes ventral to the foramen ovale and round and above the ventral tip of the falciform process. Posterior to the dorsal and proximal parts of the latter process, the ventral concavity of the cranium is filled by a fibro-venous plexus and the alisphenoid is partly visible. These features are of importance in considering the progressive enlargement of the air spaces and will be referred to in the description of other species.

In the orbital region the pterygoid sinus passes over the ventral aspect of the orbito-sphenoid, being more laterally extended than this bone and forming the proximal part of the ventral floor of the orbit. The wide infundibulum for the optic and oculomotor nerves can be seen in the figure and it will be noted that its dorsal wall is formed by the ventral wall of the orbital process of the frontal. Posterior and anterior to this infundibulum are the post-orbital and pre-orbital extensions of the pterygoid sinus. The post-orbital extension is much more limited posteriorly than in *Inia* and *Phocaena* and has, instead of the long attenuated diverticulum which in the latter two species lies under the post-orbital process of the frontal, a small, half-oval protrusion. The pre-orbital extension is also more limited than in *Phocaena* and is confined to the deep concavity which surrounds the pre-orbital foramen. There is no anterior sinus.

The middle sinus

This has been well injected and shows the typical form which the sinus takes, with few variations, in nearly every species of cetacean. The air space is exactly delineated by the tympano-squamosal recess and its lateral margin lies in the deep groove formed by the involuted margin of the glenoid fossa.

GLOBICEPHALA MELAENA

The posterior sinus

No part of the posterior sinus has been injected but its position in the saucer-like depression in the paroccipital process is marked by a dotted line (Pl. 34).

The peribullary sinus

A part of the peribullary sinus lies between the tympanic bulla and the basioccipital crest and shows the irregular, rugose form of its ventral edge. The significance of this irregular outline, which is very conspicuous in some other species, e.g. *Tursiops* (Pl. 44), may be seen by comparing it with the condition of the bone of the lateral aspect of the basioccipital crest in the primitive cetacean *Platanista* (Pl. 17). In the latter species the basioccipital crests are stout and the lateral aspect of the bone shows extensive cavitations and a minutely cancellated structure. The proximity of this finely cancellated bone to the peribullary spaces in *Platanista* suggests that the bone and air spaces are intimately connected and that the cancellation is due to resorption of bone with the progressive enlargement of the sinus. The thinness of the basioccipital crest and the rugose surface of the air sinus cast in *Globicephala* indicate that the peribullary sinus in the more specialized odontocetes has been developed at the expense of the osseous content of the basioccipital crest (see p. 80). A forward extension of the peribullary sinus can be seen occupying the deep cavity anterior to the periotic and should be compared with the fibro-venous plexus which is found in this area in *Phocaena phocoena* and *Lagenorhynchus albirostris*.

The pterygoid sinus

The relationship between the pterygoid sinus and the Eustachian tube is well shown in Pl. 34. Both structures emerge from the involucral anterior fissure of the tympanic bulla but diverge just anterior to the tip of the falciform process. The connection between the lumen of the Eustachian tube and the pterygoid sinus has been fully described by Beauregard (see p. 8). From Pl. 34 it will be seen that the Eustachian tube lies ventral to the pterygoid sinus and lateral to the basioccipital crest until it reaches the posterior margin of the choanae, thereafter passing by way of the deep notch in the pterygoid bone along the lateral wall of the posterior nares. The ventral aspect of the internal cast of this tube shown in the figure is marked by a series of obliquely-disposed, deep fissures which mark the position of those valvular folds in the lining walls of the Eustachian tube which have been fully described by Anderson, Beauregard, Boenninghaus and others. Anterior to the bulla the pterygoid sinus passes, as in the previously described species, along the mesial aspect of the ventral part of the falciform process, and round the ventral and anterior margins of the foramen ovale. Thereafter the sinus expands conspicuously and completely fills the angle formed by the mesial lamina of the pterygoid bone and the external ventral wall of the cranium. In this species the alisphenoid bone is completely covered and the pterygoid hamuli widely dilated. There are no vestiges of the lateral lamina of the pterygoid on the external face of the sinus. Close examination of this external face reveals that it is marked by very numerous, minute indentations and folds, the significance of which will be understood in relation with the histology of the sacs. As in *Lagenorhynchus* the hamuli are completely filled.

Further forward the arrangement of the sinus is very similar to that in *Lagenorhynchus albirostris*. As in the latter species, there are three distinct portions in this region; (1) a post-orbital lobe which lies along the posterior margin of the optic infundibulum but which does not, as in all the previously described species, give off a dorsally directed diverticulum under the ventral face of the post-orbital process of the frontal ; (2) an orbital part which covers the orbito-sphenoid and forms the ventral closing wall of the optic infundibulum ; (3) a pre-orbital lobe which fills the concavity round the pre-orbital foramen and extends laterally a short distance along the anterior margin of the optic infundibulum. As in the previous species the dorsal wall of this infundibulum is formed by the frontal, a considerable portion of the latter bone being visible in Pl. 34 between the pre-orbital and post-orbital lobes of the pterygoid sinus. There is no anterior sinus.

The middle sinus

The middle sinus has not been injected but its position is marked by a dotted line in Pl. 34.

GRAMPUS GRISEUS

The posterior sinus

The position of this sinus, though not well injected, can be seen from Pl. 42. The sinus occupies the concavity on the antero-ventral aspect of the paroccipital process.

The peribullary sinus

This can be seen in Pl. 42 occupying the space between the mesial aspect of the tympanic bulla and the lateral aspect of the basioccipital crests, as well as the concavity behind the falciform process. The rugose character of its external borders should be noted.

The pterygoid sinus

As in previously described species, the pterygoid sinus emerges from the tympanic bulla in conjunction with the Eustachian tube. The latter is not shown in the plate since its internal cast was so delicate and flattened meso-laterally that it became detached before the photographs were taken. Sufficient of the narial part of the tube remained to indicate that its form and direction were similar to those of the Eustachian tube of other species and have been so indicated. The sinus widens abruptly in front of the falciform process, sweeps round the ventral and anterior margins of the foramen ovale and covers the whole of the alisphenoid. In the region of the foramen ovale there are numerous, posteriorly-directed, lobulated diverticulae which pass over the dorsal margin of the foramen and become contiguous with the anterior extremity of the peribullary sinus. As in *Globicephala*, the sinus is very expansive and fills the angle between the mesial lamina of the pterygoid and the external wall of the cranium. The pterygoid hamuli are entirely filled and even more widely dilated than in *Globicephala*. In respect of the orbital extensions of the sinus there are several major differences between the arrangement in this species and that in all the previously described specimens. The lateral extension of the sinus which covers the ventral aspect of the orbito-sphenoid is very much wider and more extensive than in *Globicephala* and forms a greater part of the floor of the orbit. The post-orbital lobe is also larger and has a wide diverticulum under the post-orbital process of the frontal. The pre-orbital lobe is equally developed and is not confined merely to the concavity which surrounds the pre-orbital foramen but continues laterally almost as far as the lateral limit of the frontal. In Pl. 42 a narrow strip of the frontal bone can be seen separating the post-orbital and pre-orbital lobes and forming the roof of the optic infundibulum, but in another injected specimen (not figured) the frontal bone is obliterated in this region by coalescence or close contiguity of the two lobes. In this manner the optic nerves and muscles have been completely surrounded in the latter specimen by a continuous band of air sinus. The extremities of all the lobes hitherto mentioned show the peculiar lobulated form which was noted on the diverticulae round the dorsal margin of the foramen ovale.

The anterior sinus

It will be seen from Pl. 42 that the pterygoid sinus not only fills the deep fossa on the lateral aspect of the palatine bone (see p. 57 and Pl. 41) but extends anteriorly under the maxilla for a short distance.

The middle sinus

The middle sinus is well shown in Pl. 42, partly filling the tympano-squamosal recess. It will be noted that it consists of two lobes, one of which is directed laterally round the posterior border of the glenoid fossa, and the other directed antero-laterally round the anterior margin of the same fossa and following the anterior border of the zygomatic process of the squamosal. The whole sinus is minutely lobulated at its external borders in a manner which is characteristic of many species of odontocetes.

Tursiops truncatus

The posterior sinus

The relationship of the posterior sinus to the tympanic bulla and the depression on the paroccipital process are well illustrated on Pl. 44, and the rugosity of the external surface should be compared with that of the bone in this area.

The peribullary sinus

This is shown at its ventral extremities, mesially, between the lateral aspect of the basioccipital crest and the mesial aspect of the tympanic bulla, and anteriorly behind the curved posterior border of the falciform process. As in other species, the surface is irregularly contoured.

The pterygoid sinus

This sinus emerges from the anterior aperture of the tympanic bulla in conjunction with the Eustachian tube, the proximal end of which is shown in the plate. Here again, owing to the laterally compressed state of the tube, its lumen has not been injected but its approximate direction has been indicated. The pterygoid sinus passes over the tip of the falciform process, round the ventral and anterior margins of the foramen ovale, spreading out laterally, ventrally and anteriorly, filling the angle between the mesial lamina of the pterygoid and the ventral aspect of the cranium, and completely covering the alisphenoid. As in Risso's Dolphin there are posteriorly directed diverticula passing round the superior margin of the foramen ovale so that the mandibular branch of the 5th nerve is entirely surrounded by air space. More anteriorly the arrangement is very similar to that in *Grampus griseus*, although the pterygoid hamuli are not as widely dilated as in the latter species. The orbital, pre-orbital and post-orbital lobes are all well developed, the orbital lobe covering the orbito-sphenoid and forming a conspicuous laterally projecting ventral boundary to the optic infundibulum. The pre-orbital and post-orbital lobes are well extended and the latter spreads dorsally under the post-orbital process of the frontal. As in one of the specimens of *Grampus* the two lobes are closely contiguous and partly coalesced proximally so that no part of the frontal bone is visible between them. The optic nerve, like the mandibular branch of the trigeminal, is thus entirely surrounded by an air cavity. The contiguous pre-orbital and post-orbital lobes extend almost to the lateral limit of the frontal bone and their extremities are deeply cavitated with small, irregular diverticula as in *Grampus*.

The anterior sinus

With respect to the anterior sinus, *Tursiops truncatus* shows a more advanced state of the development of the air spaces than any of the previously mentioned species. The extent of the sinus is not fully demonstrated by the injection in Pl. 44 but its prolongation beyond the pre-orbital foramen has been indicated. The deep recess on the ventral aspect of the maxilla marks the boundary of the sinus when fully distended.

The middle sinus

Pl. 44 shows the form of the middle sinus and its exact point of emergence from the tympanic bulla. It will be noted that it originates immediately dorsal to the tympanic annulus and the sigmoid process. The sinus consists of two lobes, one passing laterally round the posterior border of the glenoid fossa, and the other following the course of the anterior wing of the tympano-squamosal recess.

DELPHINUS DELPHIS

The arrangement of the air sinuses in this species was figured by Anthony and Coupin (1930), but not described in detail. A summary of Beauregard's description is given on p. 8.

The posterior sinus

This sinus is not fully injected but its contiguity with the depression on the paroccipital process is demonstrated in Pl. 47.

The peribullary sinus

The ventral limits of the peribullary sinus are indicated in Pl. 47 lying between the mesial aspect of the tympanic bulla and the basioccipital crests, and in the cavity behind the falciform process.

The pterygoid sinus

The relationship between the pterygoid sinus and the Eustachian tube is demonstrated. The latter widens considerably after its emergence from the bulla and continues forward along the ventro-lateral border of the mesial lamina of the pterygoid, becoming narrower and more compressed meso-laterally until it reaches the notch in the latter bone. Having passed through the notch, its lumen becomes very attenuated and passes dorsally along the mesial aspect of the lateral wall of the posterior nares for a short distance, thereafter turning at first mesially and then ventrally to open into the choanae. The cast is marked ventrally by a series of oblique grooves which indicate the position of the valvular folds in the mucous membrane of the tube, (see p. 6). The pterygoid sinus widens out in front of the bulla, its ventral border lying mesial to the Eustachian tube and its dorsal border passing round the ventral and anterior margins of the foramen ovale. The alisphenoid is completely covered and there is a posteriorly directed, lobulated diverticulum which passes round the dorsal border of the foramen ovale. The mandibular nerve is thus surrounded ventrally, anteriorly and dorsally by the pterygoid sinus and posteriorly by the peribullary sinus. The pterygoid hamulus is filled by a ventrally directed lobe of the sinus which passes over the lateral aspect of the

Eustachian tube near the latter's entry into the pterygoid notch. This arrangement is well shown in Pl. 34 which figures the pterygoid sinus of *Globicephala*. The orbital portion is fairly prominent, covers the orbito-sphenoid and forms the ventral boundary of the optic infundibulum. The pre-orbital and post-orbital lobes are well extended laterally and unite above the optic infundibulum to form its dorsal boundary. The optic nerve is therefore completely surrounded by an air space as was observed in *Tursiops truncatus* and in one member of the species *Grampus griseus*. The dorsally directed diverticulum which extends over the ventral aspect of the post-orbital process of the frontal is wide, though fairly short.

The anterior sinus

In the degree of development of the anterior sinus *Delphinus delphis* exceeds every other known species of cetacean, although there is evidence from its osteological features that the recently described species *Lagenodelphis hosei* closely approaches its position. The soft parts of the latter species were not available but it may be assumed that the arrangement of the sinus would approximate to that of *Delphinus*. The anterior sinus of *Delphinus* takes the form of a wide, elongated sac which fills in the whole pre-orbital region and projects forward, tapering gradually to occupy the deep groove in the maxilla, and continuing anteriorly in the adult for about two thirds of the length of the rostrum.

The middle sinus

A small part of the middle sinus can be seen in Pl. 47, protruding from the tympanic bulla, its shape in the fully distended state being indicated by a dotted line. It fills the tympano-squamosal recess.

Mesoplodon bidens

The air sinus system of *Mesoplodon bidens* has been described by Anthony & Coupin (1930) but as this description does not emphasize the striking differences between the arrangement of the sinuses in ziphioid whales generally on the one hand, and those of other odontocetes on the other, the authors have decided to review the structure in the light of these differences. Anthony & Coupin distinguish several lobes of the pterygoid sinus but as these are in no way homologous with those found in other odontocetes their names cannot be adopted in the present work.

The posterior sinus

This is relatively inconspicuous in Pl. 12 as the sinus is not fully injected. Nevertheless its extent is confined within the boundaries of a smooth area on the pars mastoidea of the tympano-periotic. There is no evidence of the saucer-like depression in the paroccipital process.

The peribullary sinus

In spite of the close contiguity of the tympanic bulla with the basioccipital crest the ventral edge of a laterally compressed lobe of the peribullary sinus can be seen on Pl. 12 interposed between the above mentioned bones. It should be noted that its outline is quite smooth and regular, showing none of the rugosities which were seen on the edge of the sinus in many of the Delphinidae. There is no extensive excavation of the anterior aspect of the paroccipital process, the latter being massive and of a simple, nodular form. The falciform process is in close apposition with the anterior border of the tympanic bulla so that no part of the peribullary sinus is seen between the two bones, and there appears to be little distension of the anterior parts of the sinus generally.

The pterygoid sinus

With regard to the form of the pterygoid sinus *Mesoplodon bidens* differs from all the cetaceans hitherto described. It emerges with the Eustachian tube from the anterior end of the tympanic bulla and passes round the ventral and anterior borders of the foramen ovale. The superior margin of the latter foramen is not surrounded by the sinus, its wall being formed by the ventral surface of the alisphenoid bone. This posterior part of the sinus lies against the mesial lamina of the pterygoid bone and is insignificant in extent compared with the same region in the previously described species. Anteriorly, the sinus expands to form a single, great, bulbous lobe which is homologous solely with that part of the sinus which in the cetaceans already described passes ventrally to fill the pterygoid hamulus. Mesially, it is in relation to the great fossa on the lateral aspect of the conspicuously enlarged hamuli. Dorsally, it is in relation to the long narrow shelf of the pterygoid bones which stretches from the pre-orbital region to the tympanic (see p. 40). There are no traces of a lamina of bone on its exterior face and the latter is quite smooth and regular in contour, showing none of the minute lobulations which are to be found on the surface of the sinuses in all the other described species. The significance of this smoothness of contour is discussed on p. 40. There are no pre-orbital nor post-orbital lobes of the sinus nor any extension of the latter above the narrow lateral ridge of the pterygoid bone. The optic infundibulum is formed entirely of bone, its ventral aspect being bounded by part of the lateral ridge of the pterygoid and its dorsal aspect by the frontal; it is therefore true to say that none of the cranial nerves is completely surrounded by an air space, as in some of the other odontocetes.

As previously stated, there is no pre-orbital lobe of the pterygoid and therefore no anterior sinus. The pre-orbital foramen is bounded only by its associated bones.

The middle sinus

This is similar in shape to that of the other odontocete species. It emerges from the tympanic bulla above the tympanic annulus and invades the tympano-squamosal recess. Its two lobes pass respectively posteriorly and anteriorly to the glenoid fossa.

MYSTICETI

BALAENOPTERA ACUTOROSTRATA

The arrangement of the air sinus system was fully described by Beauregard (1894) but for convenience of comparison with that of the Odontoceti his account is repeated below. He states –" In order to give an account of the tympanic cavity and its annexes we made an injection of wax through the external orifice of the Eustachian tube. After solidification we sawed through the tympanic bulla horizontally and took off the whole of the lower wall. The passage of the Eustachian tube—very nearly rectilinear and directed backwards and outwards passes between the angle formed by the inferior border of the sphenoid and the digitiform process of the pterygoid. It intrudes thereafter into the vast pterygoid sinus. This sinus is therefore to be considered an enlargement of the posterior extremity of the Eustachian tube. The communicating orifice of this canal is provided with a valve, formed by a tongue of membrane hanging from the upper wall and, in the neighbourhood of the orifice, the dense fibrous tissue which covers the lower surface of the cranium and closes the sinus ventrally, is thrown into numerous folds and pockets, which we found filled with injection and are therefore continuous with the Eustachian tube. The injection filled at the same time the vast pterygoid sinus and the tympanic cavity proper. These two cavities are in communication by the anterior orifice of the bulla, or rather by the anterior extremity of the long opening situated between the two lips of the bulla. The relationship between the pterygoid sinus and the Eustachian tube on the one hand and the latter with the tympanic cavity shows that this sinus should be regarded as the homologue of the anterior sinus which we have described in the dolphins." The present writers find it more convenient to regard the whole of this structure as the pterygoid sinus since it is entirely delineated by the pterygoid bones (see p. 8). Beauregard goes on to describe how the injection passed into three other cavities.

" *No.* 2. A large cavity which corresponds with the whole of the upper and inner surfaces of the bulla but does not lie underneath it. We refer to it under the name Peribullary Sinus.

" *No.* 3. A small diverticulum situated at the posterior extremity of the bulla in the groove formed by the lower lateral border of the occipital. It is therefore a Posterior Sinus."

No. 4. The fourth sinus described by Beauregard is the conical diverticulum known as the " glove finger " which he homologized with the middle sinus of the Odontoceti. The author bases his identification on the fact that the glove finger protrudes from the tympanic annulus which in the Odontoceti appears to be divided into two segments, the upper segment forming the boundary of the proximal end of the middle sinus. It should be pointed out, however, that the glove finger is covered exteriorly by epidermis whereas the middle sinus of the Odontoceti is covered externally by periosteal tissue. Fraser & Purves (1945) demonstrated the similarity between the glove finger and the non-fibrous portion of the tympanic " membrane " of the Odontoceti, the two structures being homologized with the pars flaccida of the tympanic membrane of terrestrial mammals. The division of the tympanic annulus into two segments is peculiar to the Odontoceti and it must be assumed that the upper segment from which the middle sinus protrudes has been produced by rupture of the dorso-lateral wall of the bulla. The present writers have been unable to find any structure in the Mysticeti comparable with the middle sinus and there is no recognizable tympano-squamosal recess (see p. 9).

In this and in the previous chapter, relationship has been demonstrated between the air sinus system and the contouring of the base of the skull in a number of cetaceans. The evidence is sufficiently conclusive to enable a reconstruction to be made of the air sinus systems of species which were not available in the flesh. It should be pointed out that the indications of the distribution of air sinuses shown in Pls. 5–47, with the exception of those in which there is the direct evidence of the plastic injection, have been determined by the distribution of the smoothed areas on the ventral surface of the skull and the evidence of partial disappearance of the bones themselves. The limits of the air sacs in all the plates are indicated by a broken line and the unossified regions by white stippling. The limitations imposed by representing in two dimensions that which is three dimensional should be borne in mind when studying the plates.

The evolution of air sinuses in the Cetacea generally is discussed in the following chapter in which simplified, schematic diagrams are used to illustrate their distribution. If comparison is made between these diagrams and the photographs of the air spaces it should be remembered that the latter are viewed obliquely, whilst the former are normal to the lateral and dorso-ventral aspects.

It is the writers' opinion that however limited or extensive the various components of the air sinuses may be, they represent a system, which in its early evolutionary stages was covered by bone, and that, whether or not the osseous content of the bone remains, the closing fibrous walls of the sacs are periosteal in origin.

The absence of the conventional maxillary, frontal and sphenoidal air sinuses in cetaceans, and the general distribution of air sacs in this order, appears to give some justification to Monro's (1785) homology (see p. 5) but the more likely explanation seems to be that if the normal mammalian sinuses were ever present in cetaceans their positions have been occupied by middle ear extension.

EVOLUTION OF THE AIR SACS

Before going on to a discussion of the function of the air sinuses and their importance in connection with the inter-relationships of the Cetacea it is necessary to consider the possible mode of evolution of the sinuses from the typical mammalian middle ear. The periotic portion of the tympano-periotic bones of terrestrial mammals forms a part of the cranial wall and is closely contiguous with adjacent cranial bones. Further, the tympanic cavity is simple and circumscribed and communicates directly with the narial cavity through the Eustachian tube. The kangaroo, bat, tapir, horse and hyrax are notable exceptions to this generalization. In the Cetacea the tympano-periotic bones are excluded and more or less distant from the cranial wall, and the tympanic cavity is extended into an elaborate system of sinuses.

The constitution of the air sac system, the dissociation of the tympano-periotic bones from the skull and the modifications of the skull itself are already present in the foetus and their genetical origin is obvious. Nevertheless, these modifications can be interpreted in terms of the mechanical effect of pressure and tension on bone. The natural condition of rarification of bones is so strikingly similar to the abnormal conditions found in bone subjected to excessive mechanical stresses, that some principle such as the so-called "Baldwin Effect" must be invoked to link the natural to the abnormal. It has been recognized for a long time that of all the tissues comprising the body of an animal, with the single exception of blood, bone is the most plastic, in the sense that it is the most subject to modification under mechanical stresses. According to Weinmann & Sicher (1947) who quote Wolff's Law of transformation of bone, the effect of increased pressure or tension on bone can be summarized as follows:

"1. Increase of pressure beyond the limits of tolerance leads to destruction of bone by resorption.

"2. Within the limits of tolerance an increase of the normal forces of pressure or tension leads to formation of new bone.

"Increased pressure in such instances acts upon a bony surface which is normally subjected to pressure and able to withstand it. Such areas are often characterized by a covering of avascular tissue. Increased traction in an area adapted to traction will also lead to acquisition of bone. *Even slight pressure will lead to resorption of bone if forces are applied to an area which is normally neutral, or under tension and consequently not able to withstand pressure. One characteristic of this adaptation may be the covering of the bony surface by vascularized periosteum.*"

The most violent changes in pressure in the middle ear experienced by a terrestrial mammal are expressible in terms of small fractions of an atmosphere. In aquatic mammals a diving depth of even a few feet can bring about a rapid increase of pressure and a depth of 30 ft. increases the pressure by one atmosphere. Cetaceans are known to dive to much greater depths than that represented by one atmosphere, and it is not surprising therefore that during the acquisition of an aquatic habit a chain of evolutionary adjustments has occurred to meet the effects of the stresses imposed.

If the distribution of the muscles as described above is compared with that of the air sacs, it will be seen that there is a close association of the lobes of the sinus system with that of the insertion of various important muscles. Thus the peribullary sinus is associated with the sterno-mastoid, the middle sinus with the masseter, the pterygoid sinus with the tensor palati and lateral pterygoid muscles, the post-orbital lobe with the temporal and orbital muscles, the pre-orbital lobe and the anterior sinus with the mesial pterygoid.

As previously stated, it is considered that the regions of insertion of these muscles were originally osseous in nature, as in *Platanista*. This points to an early situation where, after the formation of an inter-laminar air space there would be pressure beyond the normal on the inter-laminar face of bones such as the pterygoid with resulting resorption of bone on that face. The lateral lamina being thus reduced in thickness would be inadequate to withstand the normal tension of the muscle, unless, in accordance with Wolff's Law, new bone were formed on the external face. It is easy to see how by such a process of resorption internally and of deposition externally gradual dilation of the pterygoid bone would take place, which itself would produce tension parallel with the plane of the lamina. The condition in which the osseous content of the lamina is completely removed indicates an end point at which the pressure effect is always in excess of that of tension.

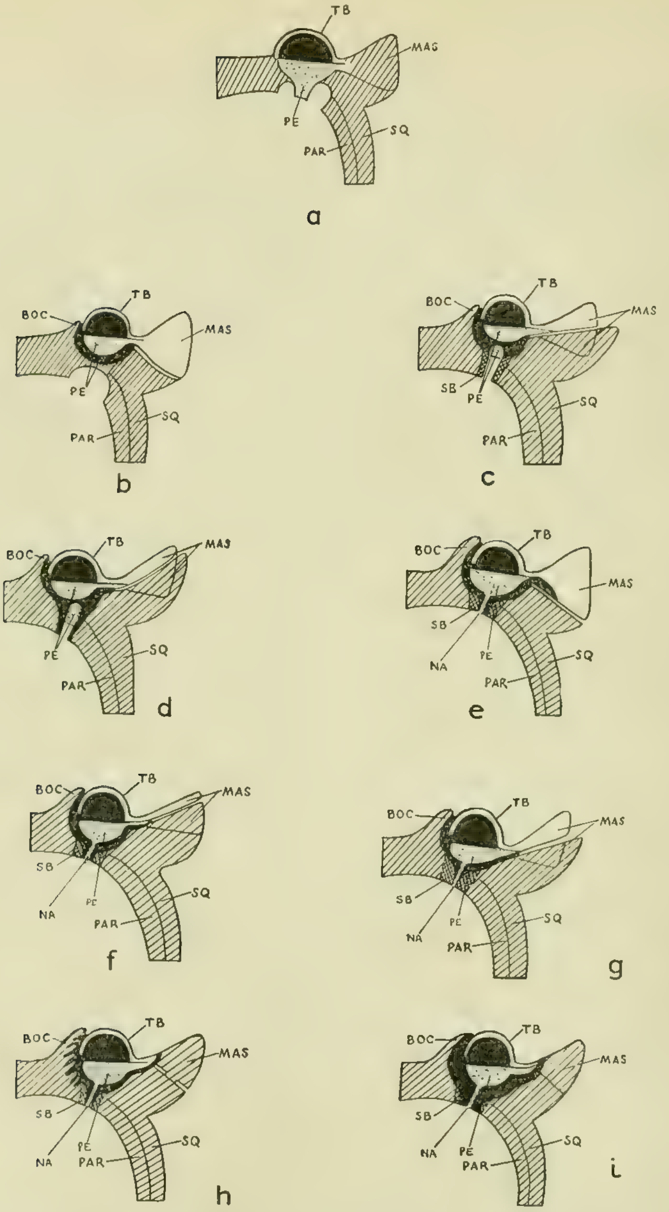
DISSOCIATION OF THE TYMPANO-PERIOTIC BONES FROM THE SKULL

The dissociation of the tympano-periotic bones from adjacent skull bones and the development of air sinuses are not of equal extent in all cetaceans. The process shows a gradation of stages involving the various genera in the Order. Text-fig. 13 gives schematic representations of the variations observed. In a terrestrial mammal, the tympano-periotic bones (TB and PE) are fused with the squamosal (SQ), and the mastoid process (MAS) is sutured with the paroccipital process (Text-fig. 13*a*). The periotic (PE) forms part of the wall of the cranial cavity but portions of it are separated from direct contact with the latter by the superior and inferior petrosal sinuses. No part of the tympanic cavity separates the periotic from cranial bones adjacent to it.

In *Caperea* (Text-fig. 13*b*) the greater part of the pars mastoidea (MAS) of the tympano-periotic is not fused but is loosely inserted between the squamosal and the basioccipital process. There is however a portion of the squamosal immediately anterior to the pars mastoidea, of a rugose and laminated appearance, very similar to that of the pars mastoidea itself. With the exception of the condition found in *Kogia* this characteristic region of bone is distinguishable to a greater or lesser extent in all the cetaceans examined. It is situated in the angle formed by the antero-lateral border of the paroccipital process and postero-lateral margin of the glenoid fossa. In *Platanista*, its anterior extent is indicated by a distinct but incomplete suture, and its posterior limit by what is commonly regarded as the squamo-paroccipital suture. In other cetaceans the anterior suture is not clearly defined although the region itself is distinguishable from the adjacent squamosal element. Since in the Mammalia generally the pars mastoidea intervenes between the zygomatic process of the squamosal and the paroccipital process, it is justifiable to regard the area of bone referred to above as a mastoid element.

The periotic of *Caperea* is in contact with the cranial cavity but is surrounded by a dorsal extension of the tympanic cavity. Another extension of the tympanic cavity is accommodated between the bulla and a raised portion of the basioccipital bone (the basioccipital crest (BOC)). Although no soft parts of *Caperea* were available for examination, the skull characteristics of the ear region (see p. 37) together with what has been observed in other mysticetes (see p. 74) indicate that the extensions of the tympanic cavity referred to above are occupied by the peribullary sinus. The postero-lateral extension of the cranial cavity (p. 29) can justifiably be regarded as occupied by the enlarged petrosal sinuses, which have become confluent as a consequence of the partial withdrawal of the periotic from the cranial wall.

In *Balaena* (Text-fig. 13*c*) the portion of the mastoid (MAS) which is fused with the squamosal (SQ) is very much greater than in *Caperea*. The base of the cranium of *Balaena* is greatly extended laterally, the paroccipital and zygomatic processes being enormous in comparison with those of *Caperea*. Correlated with this the unfused portion of the mastoid is also extended laterally and attenuated. The fused


TB
MAS
PE
SQ
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a
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i

FIG. 13. Diagrams to show progressive dissociation of tympanoperiotic bones from adjacent bones of the skull in the Cetacea.

a. Terrestrial mammal. b. *Caperea.* c. *Balaena.* d. *Balaenoptera.* e. *Kogia.* f. *Physeter.* g. *Ziphioidea.* h. *Platanista.* *i.* Delphinoidea.

Note. The black areas indicate air space.

portion of the mastoid constitutes that which in *Caperea* is continuous with the periotic so that the unfused portion appears to be of tympanic association only.

The dissociation of the tympano-periotic from the bones of the cranium is increased by the further development of the peribullary sinus. The periotic, although not separated from the cranial cavity by the above sinus, is elongated dorso-ventrayll and situated at the external end of a long infundibulum (see *Caperea* above). The petrosal sinuses appear to be confined within the limits of this infundibulum. The latter is reduced in diameter by secondary growth of its boundary bones (SB). In association with the ventral extension of the peribullary sinus the basioccipital crest (BOC) is more prominent than in the previously described genus.

In *Balaenoptera* (Text-fig. 13*d*) the amount of the mastoid (MAS) fused with the squamosal (SQ) is even more extensive than in *Balaena,* the unfused portion being a long, spatulate extension of the tympanic (TB) with a much shorter extension of the periotic (PE) fused to its dorsal face. The periotic is still more elongated dorso-ventrally than in *Balaena* but its dorsal aspect is still a component of the cranial wall. The peribullary sinus envelops the periotic as far dorsally as the cranial cavity, and, from the osteological evidence, the vascular supply of the sinus is undoubtedly merged with the petrosal sinus (see p. 29). Laterally the peribullary sinus is insinuated as an extension between the periotic pars mastoidea and the squamosal. The basioccipital crest is more prominent than in *Balaena* and its lateral face is more obviously excavated than in the last named genus.

Turning to the Odontoceti, a similar series of progressive changes can be observed which, so far as the mastoid is concerned, is parallel to that of the Mysticeti, but in the development of the peribullary sinus goes much further. Considering the Physseteroidea, *Kogia* (Text-fig. 13*e*) resembles *Caperea* in that the greater part, if not the whole, of the triangular mastoid (MAS) is not fused to the squamosal (SQ). The apparent attachment of the mastoid exclusively to the tympanic bone is due to the erosion of the periotic pars mastoidea by the peribullary sinus. The peribullary sinus not only encircles the periotic but, extending onto its dorsal surface, intervenes between it and the cranial cavity. The dorsal surface of the periotic presents the smooth, rounded appearance which is characteristic of the Odontoceti. The peribullary sinus is greatly developed between the tympano-periotic (TB and PE) and the basioccipital crest (BOC) which is more prominent than in any of the Mysticeti. The vascular system of the peribullary sinus must be considered as confluent with the petrosal sinuses (see p. 29).

In *Physeter* (Text-fig. 13*f*) a considerable portion of the mastoid (MAS) is fused to the squamosal. The unfused portion is laminated (laminations not shown in figure). Only a small portion of the periotic pars mastoidea is unfused. The peribullary sinus, as in the Odontoceti generally, envelops the periotic, intervening between it and the cranial cavity. Its vascular system is confluent with that of the petrosal and cavernous sinuses. These do not lie entirely within the cranial cavity and indeed intrude into the bulla in the form of the enigmatic cavernous tissue body which contains the "degenerate" internal carotid artery (see p. 29).

In the Ziphiidae (Text-fig. 13*g*) *Berardius*, *Mesoplodon* and *Ziphius* resemble *Physeter* both with regard to the extent of the peribullary sinus, and consequently with regard to the degree of separation of the tympano-periotic (TB and PE) from the skull. Only *Hyperoodon* differs from the remaining ziphioids in the respect that the unfused portion of the mastoid is very much reduced in its dimensions.

In some respects *Platanista* (Text-fig. 13*h*) occupies an intermediate position between the physeterids and the delphinids. Nearly the whole of the mastoid (MAS) is fused to the squamosal (SQ) although the remains of a squamo-mastoid suture are clearly discernible. The unfused pars mastoidea of the tympano-periotic represents only a small portion of the whole mastoid and in its proportions is comparable with normal delphinid condition. The part of the peribullary sinus lying above the periotic is even more restricted than in the ziphioids. The proximity of the periotic to the squamosal has given rise to the erroneous impression (Hyrtl and Yamada) that the two elements were fused together. The basioccipital crest (BOC) is similar in its general form to that of the ziphioids but its lateral aspect is extensively pneumatized by extensions of the peribullary sinus. This condition is a precursor of that common in the delphiniids in which there is such an extension of the pneumatization with the merging of individual air cavities and the further attrition of bone that the basioccipital crest is reduced to a thin lamina. The vascular system of the peribullary sinus is confluent with the petrosal venous sinuses. Above and anterior to the periotic there is a considerable hiatus in the cranial wall, except in old specimens in which the hiatus is partially filled by secondary bone. In this respect *Platanista* resembles most of the Delphinidae. *Stenodelphis* and *Inia* show a condition of the mastoid resembling that of the delphinids.

Considering the delphinid genera (Text-fig. 13*i*), whilst there is variation in the degree of development of the peribullary sinus, in general it can be stated that they show a considerably more advanced evolution of this feature. Nearly the whole of the mastoid (MAS) is fused to the squamosal (SQ), the unfused tympano-periotic pars mastoidea being reduced to a small, pointed process frequently separated from the fixed portion by an appreciable distance.

The ramifications of the peribullary sinus are so extensive that bones adjacent to it are deeply excavated. The periotic (PE) is separated from the cranial cavity by a considerable depth of pneumatic sinus.

The basioccipital is generally deeply excavated on its lateral face and thinly laminar in form, but variations are found between the rather coarse pneumatized crests of *Pseudorca* and the extremely thin and sometimes fenestrated crests of *Delphinus*.

The blood vascular system of the peribullary sinus is intimately mingled with those of the petrosal and cavernous sinuses of the cranium. A wide hiatus remains in the cranium above the periotic until advanced age when secondary bone partially blocks up the hole.

THE INVASION OF THE PTERYGOID BONE BY THE MIDDLE EAR CAVITY

With few exceptions in terrestrial mammals, the pterygoid bone (PT) (Text-fig. 14*a*) in the strict sense consists of a vertical plate of small or moderate size in relation to the alisphenoid (ALS) with which it is sometimes fused and from which it

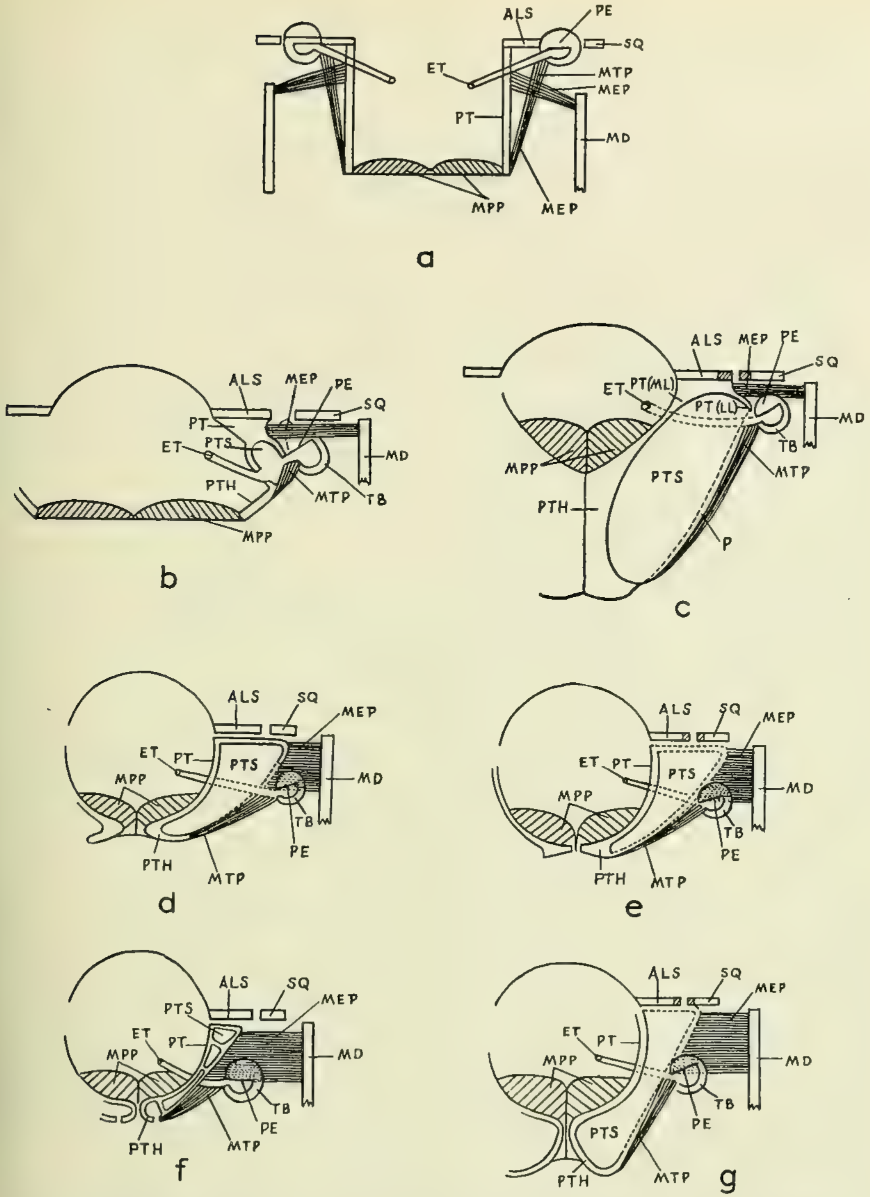
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FIG. 14. Diagrams of the pterygoid region to show invasion of the pterygoid plate by the pterygoid sinus.

a. Terrestrial mammal. *b.* Mysticeti. *c.* Ziphioidea. *d.* Monodontidae. *e.* Physteridae. f. *Platanista*. *g.* Delphinidae.

projects ventrally. The pterygoid muscles (MEP) originate on the lateral face of the pterygoid bone and are inserted on the lower jaw, to which they pass in a slightly oblique ventral direction. The tensor palati (MTP) muscle originates on the lateral aspect of the cartilage of the Eustachian tube, passes ventrally over the pterygoid hamulus whence it spreads out into a delicate aponeurosis which merges with that of its fellow on the other side. The pharyngeal muscle mass (MPP), including the levator palati, is inserted into the superior surface of the aponeurosis and together with the latter forms the soft palate. The tympano-periotic bones (PE) fused with, and forming part of the cranium, lie dorsal to the pterygoid muscles.

The pterygoid bones (PT) of the Mysticeti (Text-fig. 14*b*) are not laminar but exceedingly thickened laterally to such an extent that the alisphenoid (ALS) is obliterated from view in the ventral aspect. The tympano-periotic (TB, PE) has become displaced ventrally, is not fused with the adjacent cranial bones and has almost completely lost participation in the formation of the cranial wall. In its position it has come to lie ventral to the level of the pterygoid muscles (MEP). An extension of the middle ear cavity invades the pterygoid bone, excavating a rounded fossa (PTS) in the latter, the cavity of which communicates with the Eustachian tube (ET).

Correlated with the ventral displacement of the bulla the tensor palati muscle (MTP) is considerably shortened dorso-ventrally.

The soft palate, although reduced antero-posteriorly as compared with that of most terrestrial mammals, is relatively much wider than in the latter. The antero-posterior reduction is due to the posterior extension of the palatine bones, a process which reaches its maximum in the genus *Balaena*.

The Ziphiidae (Text-fig. 14*c*) are characterized by the great enlargement of the hamular processes of the pterygoids (PTH). The superior portion of the pterygoid bone is again greatly thickened laterally so as to cover over the ventral aspect of the alisphenoid (ALS). The extensive excavations of the pterygoid hamulus by the diverticulum from the Eustachian tube (ET) has not resulted in a symmetrical splitting of the pterygoid plate (PT). Thus whereas the medial lamina (PT (ML)) persists as a thick, bony wall, the lateral wall (PT (LL)), so far as its osseous content is concerned, is reduced to a low, ventrally directed ridge at the dorso-lateral margin of the excavation. The soft, lateral closing membrane of the excavation is the persisting periosteum (P) of the lateral lamina, the greater portion of this lateral wall of the hamulus having entirely lost its ossification. The great distension of the hamular process has resulted in displacement and modification of the muscles in its neighbourhood. Thus the external pterygoid muscle (MEP) is greatly flattened dorso-ventrally and originates above the ventrally directed ridge already referred to. The tensor palati muscle (MTP), ensheathing the lateral closing membrane of the air sac, is expanded correspondingly. The pterygoid hamuli are in close apposition in the median plane so that there is no soft palate. The palatine aponeurosis is divided by the thickness of the combined hamuli, consequently in the posterior part of the nasal channel the pharyngeal muscles (MPP) lie within the posterior nares.

The tympano-periotic bones (TB, PE), as in the Mysticeti, are displaced ventrally so that they lie below the level of the pterygoid muscle, and the modification in the form of the periotic is such that it takes no part in the composition of the cranial wall.

The mode of excavation of the pterygoid in the Delphinapteridae (Text-fig. 14*d*) shows a remarkable similarity to that of the Physeteridae (*vide infra*) in that the pterygoid hamuli (PTH) remain for the most part unexcavated and of small size. The osseous portions of the superior and lateral laminae persist to a greater extent than in the Physeteridae, since there is an osseous portion of the superior lamina below the orbito-sphenoid uniting the medial lamina with the diminished lateral lamina. As in the Physeteridae the position of the pterygoid hamulus in relation to the proximal end of the Eustachian tube is such that the main direction of the tensor palati muscle (MTP) is more horizontal than vertical.

The interpretation of the condition of the pterygoid in the Physeteridae (Text-fig. 14*e*) is based on the evidence obtainable from the skulls of *Physeter* and *Kogia* together with the information contained in Yamada's paper (1953), no soft parts being available for examination. It would seem that the excavation of the pterygoid bones is the reverse of that found in the Ziphiidae. In the latter the pterygoid hamulus is greatly enlarged and extensively excavated, while the pterygoid plate is relatively unaffected, whereas in the Physeteridae the hamulus is small, inconspicuous, and unexcavated, while the pterygoid plate is extensive in area and excavated to such a degree that the osseous content of the superior and lateral laminae of the pterygoid bone is completely absent.

From the condition of excavation of the pterygoid it can be deduced that the pterygoid muscles (MTP) must be inserted onto the periosteal closing membrane of the air sac but verification of this must await inspection of the soft parts.

The tensor palati muscle (MTP) ensheathing the air sac must be very nearly horizontal in its main direction, such is the relation of the pterygoid hamulus to the proximal end of the Eustachian tube. The pterygoid hamuli (PTH) are not quite in apposition in the middle line, but as in the Ziphiidae the palato-pharyngeal muscles (MPP) are enclosed within the posterior nares.

Platanista (Text-fig. 14*f*), so far as the pterygoid bone is concerned, is the least specialized of the Platanistidae. Indeed its condition is such that it provides (along with *Stenodelphis*) the explanation to all the successive changes found in the Cetacea, and this notwithstanding the great development of the presumably pneumatized maxillary crests. In *Platanista*, although both pterygoid plate (PT) and hamulus (PTH) are excavated, there is little inflation between the laminae, which are connected by numerous, bony trabeculae. Both the ventral and lateral laminae retain their osseous content and only the hamulus shows any degree of fenestration.

The pterygoid hamuli are closely approximated to each other in the middle line, in this feature resembling what is found in most of the Delphinidae.

No direct inspection of the pterygoid (MEP) and palatal muscles (MPP) was possible, but it can be inferred from the close approximation of the pterygoid hamuli that the palato-pharyngeal muscles are enclosed within the posterior nares. Similarly the tensor palati muscles (MTP) would appear to be more horizontally directed, as in the Physeteridae and Delphinapteridae. With regard to the pterygoid muscles it may be noted that their normal place of origin—the lateral aspect of the pterygoid plate—retains its osseous condition. This implies that the primary function of the muscles is as in the normal terrestrial mammal, that of actuating the lower jaw. It also implies that the articulation of the lower jaw must be similar to that of the terrestrial mammal. It is interesting to note that Anderson (1879, p. 433) observed in a specimen of 6½ ft long that "the jaws are capable of great extension, opening at their tip . . . to 13 inches". The size of the zygomatic process of the squamosal similarly indicates that the masseter muscle is not reduced in size as in the delphinids. The presence of a mandibular articular capsule is conjectural but seems very likely.

In the Phocaenidae and Delphinidae (Text-fig. 14*g*) both the plate (PT) and the hamulus (PTH) of each pterygoid bone are excavated, and inflated to a greater or lesser extent. The lateral and superior laminae of the pterygoid show a diminution of their osseous content, which however, is variable from genus to genus. According to the degree of distension of the pterygoid plate the ventral aspect of the alisphenoid (ALS) is exposed to a greater or lesser extent. The approximation of the hamuli to each other in the middle line is also similarly variable, the degree of approximation depending to a large extent on the state of inflation of the hamuli. The final expression of this process can be seen in *Delphinus delphis* in which the greater part of the pterygoid musculature (MEP, MTP) is attached to the persisting, non-osseous, periosteum of the lateral lamina. Due to the expansion of the pterygoid hamuli in a ventral direction, the tensor palati muscles (MTP) retain more of their vertical orientation, although they are greatly extended antero-posteriorly. The naso-pharyngeal muscle mass (MPP) lies within the posterior nares and is separated from the ventral aspect of the aponeurosis by the pterygoid air spaces.

SYSTEMATIC ARRANGEMENT

The descriptions and figures given in the foregoing section are intended to convey an impression of the average differences in the middle ear air sac system between the families of the Cetacea. There is however also intergeneric variation, which is considered to be significant and which in some families shows a serial gradation of specialization.

Text-figs. 15–21 show a schematic representation of the splitting of the pterygoid bone in the Cetacea. The diagrams in the left hand column are of the lateral aspect of the pterygoid region. The right hand column shows an antero-posterior view of the same region. In the diagrams the thick black line represents pterygoid bone, the dotted line (except in Text-fig 15*b*′) indicates those parts of the pterygoid bone from which the osseous content is absent, leaving periosteal tissue. The peribullary sinus which is derived from the tympanic cavity is shown in the diagrams but not discussed.

Text-figs. 22–25 show the dorso-ventral views of the sinus system dissociated from the skull.

Text-fig. 15*a* shows schematically the inter-relationship of the alisphenoid (ALS), palatine (PAL), maxilla (MAX), orbito-sphenoid (OS), the pterygoid plate (PT), the tympanic bulla (TB), optic (NO) and adjacent foramina, the foramen ovale (NM) and the mandibular branch of the 5th nerve, in some terrestrial mammals. Text-fig. 15*a′* is an antero-posterior view showing the inter-relationship of the pterygoid plate, basioccipital (BO), alisphenoid 5th nerve branch, foramen ovale and squamosal.

MYSTICETI

Text-fig. 15*b*, *c* shows diagramatically these relationships in *Caperea*. The tympanic cavity and Eustachian tube form a wide diverticulum which invades the pterygoid plate, and the tympano-periotic is withdrawn from direct contact with the cranial cavity. The pterygoid has become greatly thickened laterally, enveloping the mandibular branch of the 5th nerve in a deep fissure, the lips of which are in contact in a pterygoid to pterygoid suture. The nerve has been partially deflected simultaneously in a slightly anterior direction, by the forward extension of the diverticulum i.e. the pterygoid sinus. It should be noted that at this stage there is no lateral deflection of the 5th nerve branch (Text-fig. 15*b′*).

In *Balaena* (Text-fig. 15*c*) the pterygoid sinus (PTS) extends anteriorly beyond the level of the foramen ovale (NM), and the pterygoid plate (PT) is expanded laterally to a greater extent than in *Caperea*. These factors have produced a lateral as well as forward deflection of the 5th nerve branch (Text-fig. 15*c′*). That part of the pterygoid which would have covered the 5th nerve branch posteriorly has disappeared owing to the extension of the sinus dorsally. The 5th nerve branch is partially enclosed within a channel formed dorsally by the alisphenoid (ALS) and ventrally by the superior lamina of the pterygoid plate. A ventrally-directed extension of the squamosal, the falciform process (FP), lateral to the lateral pterygoid plate deflects the 5th nerve branch to its original ventral direction.

In *Caperea* the pterygoid hamulus (PTH) remains rather small but in *Balaena* it forms a wide, mesially-directed shelf.

In *Eschrichtius* (Text-fig. 15*d*) the pterygoid sinus is similar to that of *Balaena* in its posterior part whilst anteriorly it projects forward to an extent comparable with *Balaenoptera*. The falciform process (FP) is not as prominent as in *Balaena*. The mesial lamina of the pterygoid is distended mesially as well as laterally (Text-fig. 13*d′*).

Text-fig. 15*e* shows the condition in the Balaenopteridae (see also Pl. 7). The diverticulum of the Eustachian tube is more elongated and, with reference to the position of the foramen ovale, has extended anteriorly as compared with its limits in the Balaenidae. The superior lamina of the pterygoid plate (PT) completely covers the ventral aspect of the alisphenoid (ALS). Again the 5th nerve branch (NM) is deflected in a lateral direction (Text-fig. 15*e′*) and is completely enclosed within a bony tube formed ventrally by the superior lamina of he pterygoid and dorsally by the alisphenoid. The nerve is directed ventrally by an even greater development of the falciform process (FP). The falciform process bifurcates antero-posteriorly round the 5th nerve branch, thus the latter has its exit from the side of the skull formed by a second bony tube. Text-fig. 15*e′* also shows the mesial dilation of the pterygoid plate which is absent in *Balaena*. The pterygoid hamulus

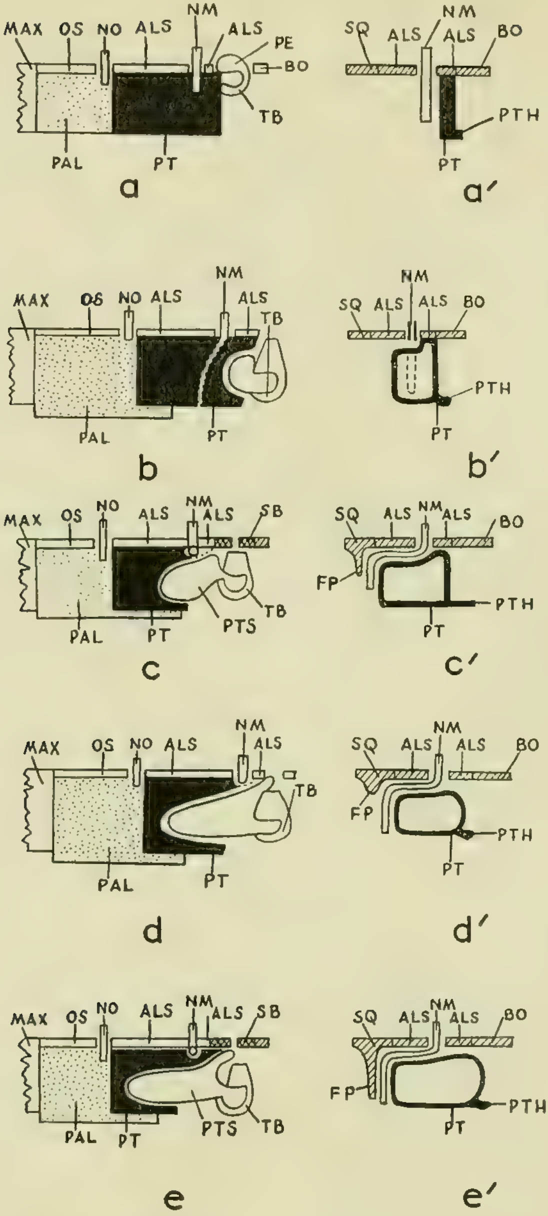
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FIG. 15. Schematic diagrams showing the progressive invasion of the pterygoid bone by the pterygoid sinus in *a* (longitudinal section), *a′* (antero-posterior transverse section), terrestrial mammal; b, b′, *Caperea*; c, c′ *Balaena*; d, d′ *Eschrichtius*; e, e′ *Balaenoptera*.

(PTH) is relatively small and, as in *Balaena*, unexcavated. Text-fig. 22 *a–d* shows the gradual development of the air sacs in the genera referred to above.

ODONTOCETI

ZIPHIOIDEA

Text-fig. 16*a* shows diagramatically the condition existing in the Ziphioidea. The distension of the pterygoid bone shows a distinct advance on the condition found in the Mysticeti. Thus the pterygoid hamulus is so extended anteriorly that it passes beyond the anterior limit of the alisphenoid (ALS), passes below the orbitosphenoid (OS) and the optic foramen (NO), compresses the palatine (PAL) antero-posteriorly and at its anterior limit makes contact with the maxillary (MAX), dividing the palatine into dorsal and ventral components. The superior lamina is fenestrated, exposing a small area of palatine. The pterygoid hamulus also extends posteriorly under the foramen ovale (NM). Its freely projecting, postero-ventral portion extends ventrally to the level of the basioccipital (BO).

Above the inflated pterygoid hamulus, in the region of the optic foramen, the undivided pterygoid plate persists, and to it the pterygoid muscles are attached (see p. 82).

The 5th nerve branch (NM) (Text-fig. 16*a*′) is directed laterally by the thin superior lamina of the pterygoid hamulus. Its more distal portions are not enclosed within a bony tube as in the Mysticeti since the whole of the osseous content of the lateral lamina is lacking and the falciform process is reduced to a slender spine. The condition of the pterygoid just described is common to all the ziphioids with negligible variation.

The air sac development is shown in Text-fig. 22*e* (see also Pls. 8–12).

MONODONTOIDEA

In *Monodon* the pterygoid hamuli remain unexcavated, inflation being confined to the pterygoid plate (Text-fig. 16*b* (and Pls. 13 and 14)). The pterygoid does not extend so far forward as to bifurcate the palatine but there is some resorption at the anterior limit of the bone so that, in the prepared skull, the palatine is exposed.

A new feature is a small, anteriorly projecting diverticulum which cavitates the alisphenoid bone behind and above the foramen ovale. As a result the portion of the alisphenoid posterior to the foramen ovale is raised in level above the remainder of the alar process and the tympano-periotic consequently is further removed from the cranial cavity.

The 5th nerve branch (Text-fig. 16*b*′), after emergence from the cranium, is not (for the most part) enclosed within a bony infundibulum because of the loss of the alisphenoidal part of the superior lamina of the pterygoid plate and because of the great reduction in size of the falciform process. There is, however, the beginning of a new infundibulum formed from the alisphenoid.

More anteriorly (Text-fig. 16*b*″) considerable parts of the ossified superior and lateral laminae remain.

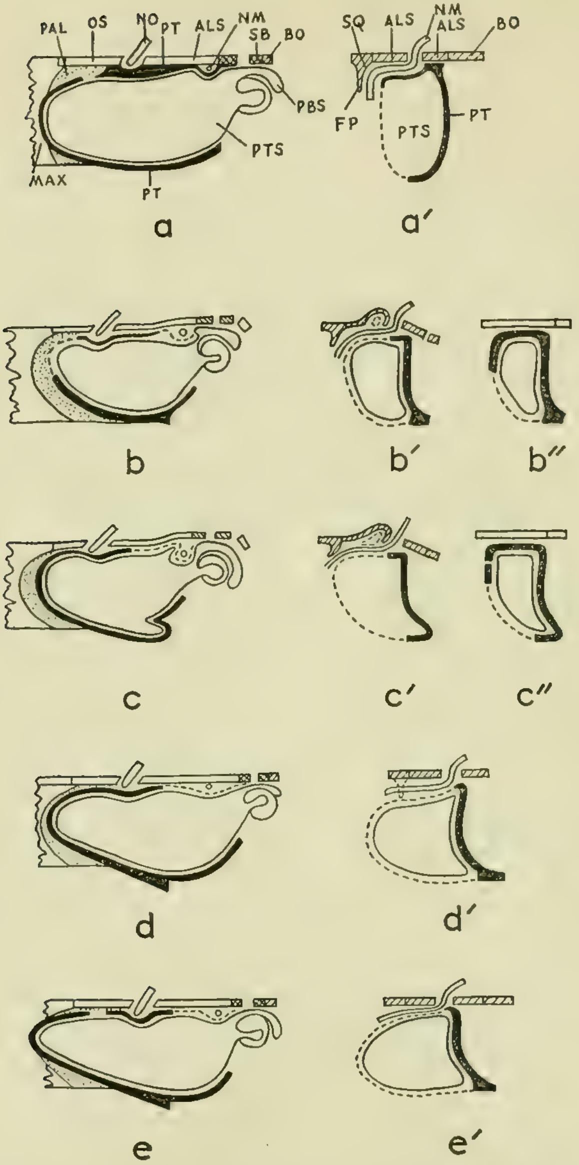
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FIG. 16. Schematic diagrams showing invasion distention and resorption of the pterygoid bone by the pterygoid sinus in *a* (longitudinal section), *a′* (transverse section). Ziphioidea ; *b*, *b′* and *b″* (further rostral than *b′*) *Monodon* ; c, c′ c″ *Delphinapterus* ; d, d′ *Kogia* ; e, e′ *Physeter*.

The other existing representative of the Monodontoidea, *Delphinapterus* (Text-fig. 16*c* and Pl. 15) differs from *Monodon* mainly in having the pterygoid hamuli slightly inflated, in this approximating to the condition generally encountered in the Delphinidae. As in *Monodon* the alisphenoid is excavated behind the foramen ovale and in this region is raised in level above that of the rest of the bone. A posterior extension of the pterygoid periosteum is in contact with this excavation above the foramen ovale.

The 5th nerve branch (Text-fig. 16*c*′) shows approximately the same condition as in *Monodon*. More anteriorly (Text-fig. 16*c*″) there is greater resorption of the lateral lamina than in *Monodon*. The hamulus, as shown in this and the previous figure, is excavated.

The diagram of the dissociated air sacs are shown in Text-fig. 22*f* and *g*.

PHYSETEROIDEA

In contrast with the Ziphioidea, in the Physeteroidea (Text-figs. 16*d* and *e* and Pl. 16) the splitting of the pterygoid is restricted to the pterygoid plate and does not involve the hamulus. The degree of anterior extension of the pterygoid plate in *Physeter* (Text-fig. 16*d*) is similar to that effected by the hamular element in the Ziphiidae except that the palatine bone, although compressed, is not divided anteriorly. The occipital crest (not shown in the figure) is reduced in size by a backward projection of the mesial lamina of pterygoid plate, and it is reasonable to assume that the superior lamina has been similarly extended and that the wide exposure of the alisphenoid in the cleaned skull is due to the loss of the osseous content of the superior lamina.

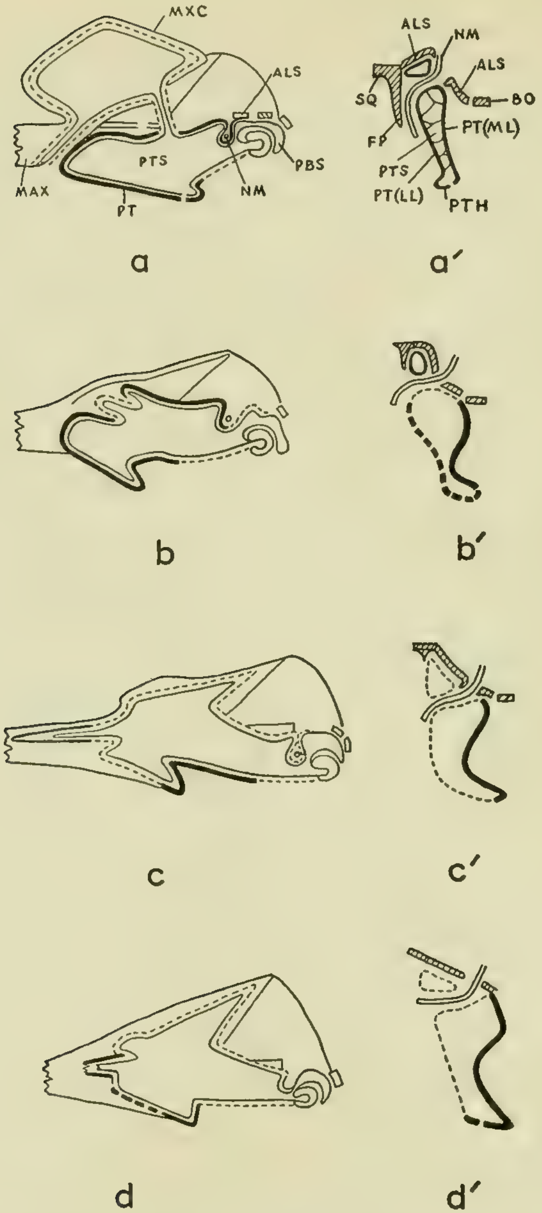
The 5th nerve branch (Text-fig. 16*d*′) is not enclosed within any bony tube lateral to its emergence from the alisphenoid since the osseous content of the superior lamina of the pterygoid is lacking. Similarly the distal portions of the nerve are not surrounded by bone because the lateral lamina is no longer ossified. The falciform process is reduced to a diminutive plate. The lateral aspect of the mesial plate is convex which is in contrast to the concavity found in this region in the ziphioids.

Kogia (Text-fig. 16*e*) is essentially similar to *Physeter* in the condition of splitting of the pterygoid, except that in its forward extension the latter divides the palatine into a dorsal and a ventral component. This condition is comparable with that found in the Ziphiidae except that in the latter it is the hamular portion of the bone, which is involved. The 5th nerve branch (Text-fig. 16*e*′) is not enclosed in any bony channel after emergence from the alisphenoid and there is no remaining vestige of the falciform process.

The diagrams of the dissociated air sacs are shown in Text-fig. 22*h* and *i*.

PLATANISTOIDEA

The members of the family Platanistidae (Text-fig. 17 and Pls. 18–23) show relatively primitive features so far as the ventral region of the pterygoid bone is concerned but they approximate more closely to the conditions found in the delphinids than to the Physeteridae, Ziphiidae or any of the Mysticeti. The chief characteristic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d
d′

FIG. 17. Schematic diagrams showing invasion, distention and resorption of the pterygoid bone by the pterygoid sinus in *a* (longitudinal section), *a′* (transverse section), *Platanista* ; b, b′, *Stenodelphis* ; c, c′, *Inia* ; d, d′ *Lipotes*.

of *Platanista* (Text-fig. 17*a*) is that each pterygoid (PT) completely overrides the palatine and extends onto the posterior end of the maxilla (MAX). The pterygoid hamuli, although small, are completely excavated and to some extent fenestrated. The mesial (PT (ML)) and lateral (PT (LL)) laminae of the pterygoid plate are connected by bony trabeculae (Text-fig. 17*a*′). In addition to the forwardly projecting cavitation of the alisphenoid behind the foramen ovale, there is a posteriorly projecting diverticulum of the pterygoid bone which comes into contact with the alisphenoidal cavitation above the foramen ovale. The two diverticula do not merge where they come together, two very thin bony laminae having been observed which separate them. The infundibulum of the optic nerve is very greatly reduced.

The internal architecture of the characteristic maxillary crests (MXC) of *Platanista* so resembles that of the interlaminar region of the pterygoid that it is reasonable to suppose that the cavitation of the pterygoid is continuous with that of the maxillary crests. Bony channels connect the two regions and, in the series of cetacean skulls examined and described in this paper, there is plenty of evidence of the extensibility of the pterygoid beyond its obvious limits (see for example Text-fig. 19*a* of *Pseudorca* where portions of the pterygoid have penetrated the orbital and preorbital regions). *Platanista* can be regarded as an extreme example of this process. Indeed it would not be unreasonable to regard the development of the maxillary crests as a consequence of a corresponding extension of the pterygoids. A diverticullum of this extension passes obliquely forward on either side of the base of the rostrum splitting the bone in this region into dorsal and ventral laminae which are connected mesially, and probably laterally also in the living animal, by bone. In *Inia*, as will be described below, a slender extension of the pterygoid sac projects into the rostrum, whether this is so in *Platanista* has yet to be ascertained.

There is no indication in *Stenodelphis* (Text-fig. 17*b*) of the assumed extension in *Platanista* of the pterygoid sinus system onto the dorsal aspect of the skull. Apart from this, the ramifications of the pterygoid bone on the ventral aspect of the skull show an advance on *Platanista*. Each extends forward beyond the limit of the orbitosphenoid onto the lateral aspect of the frontal. It also invades the orbit in the region normally occupied by the prominent orbital nerves and muscles. This condition should be compared with that found in *Pseudorca* in which the eye and its muscles are fully functional. The pterygoid hamuli are more pronouncedly excavated and inflated than in *Platanista*. The posterior diverticulum of the pterygoid sinus which passes dorsal to the foramen ovale is more dorsally situated in relation to the latter than in *Platanista*.

The 5th nerve branch (Text-fig. 17*b*′) issuing from the cranial cavity appears to be bounded dorsally by the very thin, bony lamina which encloses the small pterygoid diverticulum passing posteriorly above the foramen ovale. The corresponding ventral boundary of the nerve is not ossified. The lateral lamina of the pterygoid retains most of its osseous content although it is extensively fenestrated. The dorsally-directed spread of the pterygoid is accompanied by a corresponding dorsal deflection of the wing of the alisphenoid.

The distribution of the pterygoid sinus system in *Inia* has been obtained largely from radiographic evidence, the bony element of the region being so greatly lacking (see p. 45). In this species (Text-fig. 17*c*) the whole of the ventro-lateral aspect of the frontal is ensheathed by an extension of the sinus system which was presumably enclosed within a corresponding extension of the pterygoid bone, the osseous element of which has disappeared. In addition to the excavation and extension of the pterygoid hamulus, there is a slender, elongated extension of the sinus into the maxillary bone of the rostrum. The exact disposition of the diverticula round the foramen ovale cannot be ascertained but presumably they are in very close contact with each other, the 5th nerve on emergence from the cranium being completely surrounded by a non-ossified boundary. Text-fig. 17*c'* shows the remaining, ossified, mesial lamina of the pterygoid. The extensive loss of osseous content in the lateral and dorsal laminae is noteworthy. The diverticulum of the pterygoid sinus above the foramen ovale is much larger than in *Stenodelphis* and is without osseous content in its walls.

The distribution of the air sinus system in *Lipotes* is very similar to that of *Inia*. Noteworthy differences are that more of the osseous content of the pterygoid hamulus persists and that the post-orbital extension is wider and larger. In the absence of soft parts it is presumed that the anterior extremity of the sinus system invades the rostrum (Text-fig. 17*d*, *d'*).

The diagrams of the dissociated air sacs in the Platanistoidea are shown in Text-fig. 23*a–d*. The conjectured maxillary air sac of *Platanista* is not shown in Text-figure 23*a*.

DELPHINOIDEA

Consideration of the splitting of the pterygoid in the Delphinoidea begins with an examination of the conditions found in the Phocaenidae, because the average condition in this family is less specialized than in the Delphinidae, particularly with respect to the portions of the pterygoid on the ventral aspect of the skull. In *Phocaena* (Text-fig. 18*c*), as in *Inia*, there is an extension of the pterygoid sinus under the post-orbital process of the frontal (see also Pl. 27), and another pre-orbital extension, which in *Inia* is confluent with the post-orbital because of the reduction in size, in the latter, of the optic nerve and muscles. In *Phocaena* the optic nerve and muscles are fully functional and lie between the two diverticula. An extension of the pre-orbital diverticulum passes dorso-caudally between the frontal and maxilla; the fossa formed by this diverticulum being a characteristic feature in the phocaenid skull.

Another diverticulum in front of the foramen ovale projects posteriorly and mesially, producing a cavitation of the alisphenoid in which no osseous trace of the pterygoid remains. A ventral curving of the posterior margin of the alisphenoid posteriorly to the diverticulum just referred to, separates the latter from the peribullary sinus. A bony bridge between the hinder margin of the alisphenoid and the hinder margin of the palatine represents the remaining portion of the lateral lamina of the pterygoid (Text-fig. 18*c'*).

The 5th nerve branch, on emergence from the cranial cavity, is surrounded not by bone, but by the periosteal closing walls of the sinus, except in the vicinity of the falciform process where the dorsal aspect of the nerve is in contiguity with the

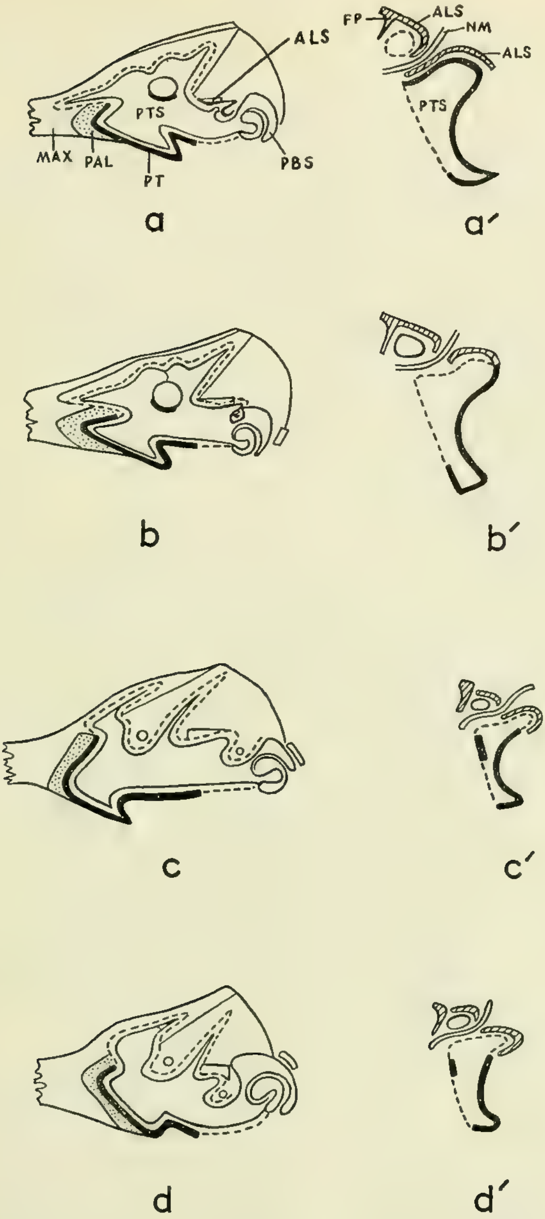
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FIG. 18. Schematic diagrams showing invasion, distention and resorption of the pterygoid bone by the pterygoid sinus in *a* (longitudinal section), *a′* (transverse section), *Steno*; b, b′ *Sousa*; c, c′ *Phocaena*; d, d′ *Neomeris*.

ventrally-directed, posterior margin of the alisphenoid. The figure (18*c*′) shows the mesial cavitation of the alisphenoid, not the more lateral, ventrally directed portion.

The pterygoid hamuli are excavated by the sinus but are not greatly inflated. Anteriorly they do not override the palatines which form an appreciable part of the palatal area of the skull.

In general, the condition of the pterygoid and its associated sac in *Neomeris*(Text-fig. 18*d* and Pl. 28) are similar to that of *Phocaena*. The pre-orbital diverticulum is more prominent, its extension between frontal and maxillary more slender. The posteriorly projecting diverticulum anterior to the foramen ovale is shorter antero-posteriorly and occupies a deeper concavity of the wing of the sphenoid. The anterior lobe of the peribullary sinus extends further anteriorly above the foramen ovale. The palatines are as in *Phocaena*. The pterygoid hamuli are only partially excavated and are uninflated. The small bony bridge (Text-fig. 18*d*′) of the lateral lamina of the pterygoid plate remains.

The 5th nerve branch on emergence from the cranial cavity is surrounded dorsally and posteriorly by the peribullary sinus, ventrally and anteriorly by the pterygoid diverticulum in the region of the alisphenoid.

The diagrams of the dissociated air sacs of the Phocaenidae are shown in Text-fig. 23*g* and *h*.

The sub-family Orcinae, and particularly *Pseudorca*, provides most useful evidence about the origin of ramifications of the sinus system. Like *Stenodelphis* (see above p. 91), *Pseudorca* specimens demonstrate how the non-osseous closing membranes of the pterygoid system are secondary to a phase during which the osseous content of the ramifying pterygoid bone is still present (see Pls. 29 and 30). Thus there are individuals in which the pre- and post-orbital diverticula are completely enclosed in a bony armour. In other specimens again, the bony armour is heavily fenestrated and frequently represented by a bony cagework. (This last is the condition in the specimen figured in Pl. 30). At the other end of the scale there are specimens in which the osseous content of the pre-orbital extensions and the lateral lamina of the pterygoid is wanting. Text-fig. 19*a* gives a generalized picture of the *Pseudorca* condition and shows the relatively small pre-orbital and post-orbital diverticula.

The posteriorly projecting diverticulum of the pterygoid air sac passes round the dorsal margin of the foramen ovale (NM) and the implication of the peribullary sinus (PBS) in the investment of the 5th nerve branch is very small. The bony, dorsal lamina of the pterygoid is fenestrated to a greater or less extent in different individuals.

The pterygoid hamulus is excavated and much inflated but only slightly overrides the palatine (PAL).

The hamulus projects mesially to a greater extent than in previously described genera (Text-fig. 19*a*′) so that the mesial border of the one hamulus closely approximates to that of the other.

The 5th nerve branch on emergence from the skull is frequently enclosed in a cagework of small, bony trabeculae which represent the last remnants of a bony infundibulum.

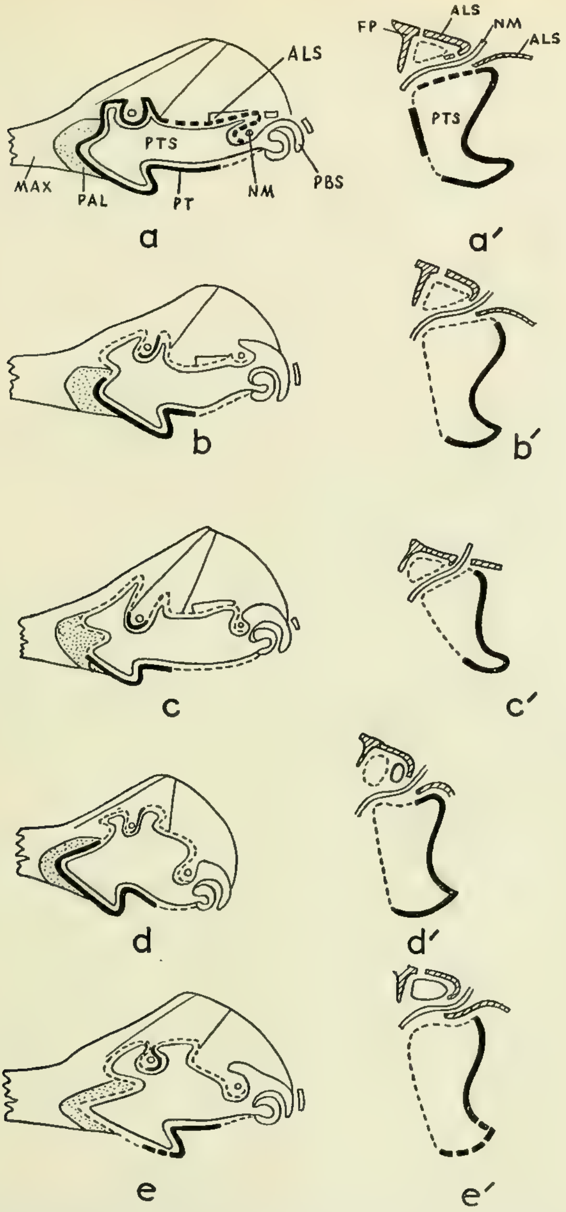
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FIG. 19. Schematic diagrams showing invasion, distention and resorption of the pterygoid bone by the pterygoid sinus in *a* (longitudinal section), *a′* (transverse section), *Pseudorca* ; b, b′ *Orcinus* ; c, c′ *Orcaella* ; d, d′ *Globicephala* ; d, d′ *Feresa*.

The osseous content of the lateral lamina of the pterygoid appears to be wanting, but external to the pterygoid periosteal closing membrane, is a bony bridge consisting of a plate formed by a posteriorly directed extension of the palatine and an anteriorly extending process from the base of the falciform process (see pp. 35–37 *supra*).

The condition of the sinus system in *Orcinus* (Text-fig. 19*b* and Pl. 31) is in general similar to that of *Pseudorca* but with certain modifications. Thus, the pre-orbital sac is enlarged in size relative to the post-orbital, both sacs are expanded in a lateral direction and the anterior sac extends onto the palatal surface of the maxilla (its anterior limit being difficult to define in the prepared skull). The fossa which gives access to the maxillary foramen is very much enlarged relative to that of other dolphins. It is confluent with the bony cavity which houses the pre-orbital sac, but the significance of their contiguity is not understood.

The peribullary sinus projects anteriorly as far as the anterior margin of the foramen ovale.

As in *Pseudorca* the palatine is not extensively over-ridden by the pterygoid.

The extensive disappearance of the osseous content of the superior and lateral laminae is indicated in Text-fig. 19*b*′. The hamuli are extensively excavated and inflated. They meet in the middle line.

The 5th nerve branch on emergence from the cranial wall is entirely surrounded by air sac derived from the peribullary and pterygoid sinuses.

In *Orcaella* (Text-fig. 19*c* and Pl. 32) the pre-orbital cavity is conspicuously wide and does not become constricted as it passes dorsally behind the maxilla. A diverticulum of the pre-orbital extension of the air sac projects forward and overlaps the ventral surface of the maxilla at the base of the rostrum. In the sphenoidal region there is no clearly delineated line of demarcation between the posterior limit of the pterygoid system and the peribullary sinus. Any division that exists between these systems must be membranous. The pterygoid hamulus overrides the palatine to such an extent that the latter is divided into two portions, dorsal and lateral respectively.

The pterygoid hamuli (Text-fig. 19*c*′) are widely separated, excavated and partially dilated. There is no trace of an osseous lateral lamina. The 5th nerve branch is entirely surrounded by air sac. The respective participation of the peribullary and pterygoid systems in the investment of the nerve cannot be assessed in the absence of soft parts. The falciform process is considerably reduced and attenuated in correspondence with the increased development of sinuses.

In the genus *Globicephala* (Text-fig. 19*d*, frontispiece, and Pls. 33 and 34) lateral expansion of the sphenoidal portions of the pterygoid sac has taken place. The orbital lobes appear to be relatively insignificant. The alisphenoid has been completely over-ridden by the pterygoid sac and in its lateral aspect presents only the edge of a thin lamina.

A posteriorly projecting process of the sphenoidal part of the pterygoid sac passes dorsal to the foramen ovale and superior to the anterior tip of the peribullary sinus. Anteriorly the pterygoids do not greatly override the palatines so that a fairly wide band of the latter is exposed on the palate. The palatine bones are themselves excavated by the forward extension of the hamular cavities.

The osseous content of the dorsal lamina persists (Text-fig. 19*d*) as a shelf, narrowing from below the orbito-sphenoid to disappearance below the alisphenoid. No trace remains of a bony, external lamina.

The pterygoid hamuli are completely excavated and widely dilated (Text-fig. 19*d*′). They are in contact in the middle line.

On emergence from the cranium, the 5th nerve branch is surrounded proximally by a bony infundibulum but more distally it is surrounded by extensions of the peribullary and pterygoid sinuses.

The genus *Feresa* may be considered conveniently with the *Orcinae* because of its apparent affinity with the latter, although in some respects it bears resemblance to *Grampus griseus* also.

The post-orbital and sphenoidal portions of the pterygoid sacs are greatly enlarged (Text-fig. 19*e* and Pl. 35). The pre-orbital and post-orbital sacs are apparently in contact above the optic nerve. Not only has the bony content of the dorsal lamina of the pterygoid disappeared, but the wide, ventrally exposed alisphenoid is so reduced in thickness that its lateral aspect, in the temporal fossa, is extremely narrow. The peribullary sinus passes forward above the foramen ovale. The pre-orbital sac overlaps onto the palatal aspect of the maxilla to form the anterior sac.

The palatine bones are widely exposed but very deeply excavated by the pterygoid sacs. This excavation is continued forward so that the posterior aspect of the maxilla is also involved and both palatine and maxilla are fenestrated on the palatal aspect.

The superior and lateral laminae of the pterygoid (Text-fig. 19*e*′) have lost their osseous content. In both of the British Museum specimens and in Yamada's (1953) figured specimen, the posterior portions of the pterygoid hamuli are missing. The heavily fenestrated portions that remain, together with the incompleteness of the hamuli, are an indication of the extent to which resorption has proceeded in this genus.

The 5th nerve branch, medially to the falciform process, is surrounded by air sac, but proximally an infundibuliform extension of the alisphenoid invests it.

The dissociated air sacs of members of the Orcinae are shown in Text-fig. 24 *a–e*.

The pre-orbital and post-orbital diverticula of the pterygoid system in *Cephalorhynchus heavisidei* (Text-fig. 20*a* and Pl. 36) approximate to each other superiorly to the optic foramen to a greater extent than was evident in any of the Orcini with the exception of *Feresa*. These lobes have a tendency to spread laterally rather than vertically, giving them greater width than height, the post-orbital lobe extending posteriorly as in *Phocaena* but not to the same degree. The peribullary sinus (PBS) extends anteriorly above the foramen ovale but a well defined bony ridge of the alisphenoid separates it from the posterior limit of the pterygoid system. Each palatine bone (PAL), anterior to the pterygoid (PT) is widely exposed and not overridden by the latter.

The pterygoid hamuli (Text-fig. 20*a*′) are widely excavated and inflated, they also approximate to each other in the middle line. The 5th nerve branch (NM) on emergence from the cranium is completely surrounded by air sinus; posteriorly and dorsally by the peribullary, anteriorly and ventrally by the pterygoid.

C. commersoni (Text-fig. 20*b* and *b*′) is very closely comparable with *C. heavisidei* in the general arrangement of the sinus systems. One or two differences may however

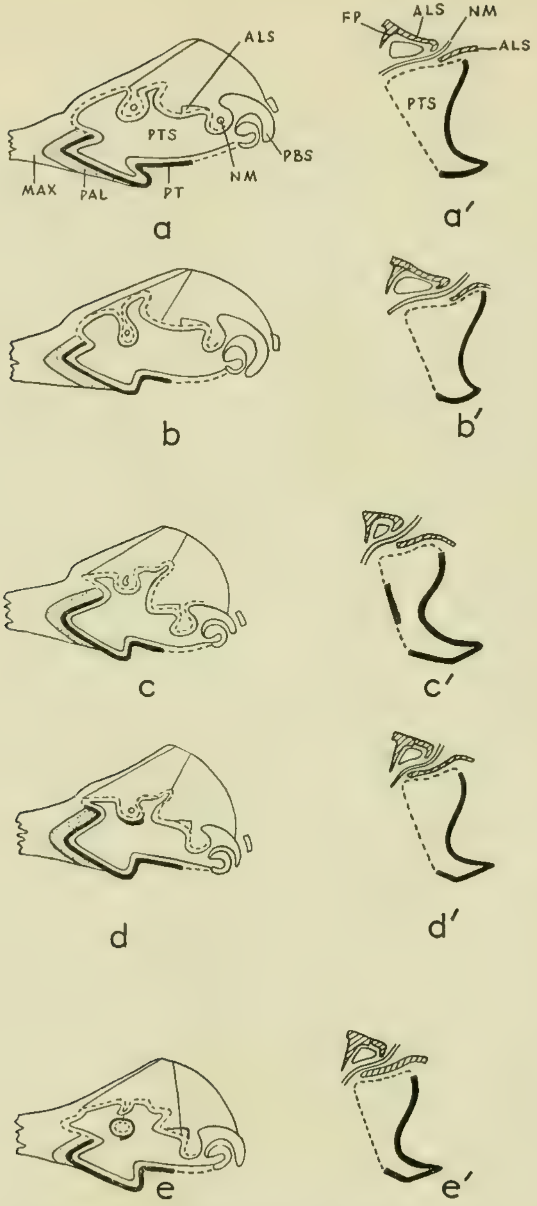
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Fig. 20. Schematic diagrams showing invasion, distention and resorption of the pterygoid bone by the pterygoid sinus in *a* (longitudinal section), *a′* (transverse section), *Cephalorhynchus heavisidei* ; b, b′ *C. commersoni* ; c, c′ *Lagenorhynchus albirostris* ; d, d′ *L. acutus* ; e, e′ *L. obscurus*.

be noted. The pre- and post-orbital diverticula are in closer approximation to each other than in *C. heavisidei* because of the disappearance, on the under surface of the orbital process of the frontal, of a bony ridge, which in the latter species forms a barrier between the two diverticula. The pre-orbital diverticulum does not extend vertically between the frontal and maxilla as in *C. commersoni*.

The air sinus system of *Cephalorhynchus* dissociated from the skull is shown in Text-fig. 24*f*.

The genus *Lagenorhynchus* is one about which information regarding the air sacs has been obtained from plastic casts of *L. albirostris* (see p. 66), but for comparative purposes it is necessary to include it in the series of diagrams.

The pre-orbital and post-orbital sacs of this species (Text-fig. 20*c* and Pl. 38) are relatively small and of about equal development, although the latter has a small posterior extension onto the posterior face of the orbital process of the frontal. They do not meet above the optic nerve. There is nothing in the nature of an anterior sinus. In the sphenoidal region the sacs do not entirely cover the ventral aspect of the alisphenoids, which are quite stout, and present a broad lateral surface in the temporal fossa. The anterior portion of the space normally occupied by the peribullary sinus is filled with a complex of veins, and by very slender, bony trabeculae with air spaces between.

Ventrally and anteriorly the pterygoids override the palatines so that only a thin strip of the latter are exposed on the palate.

The dorsal lamina (Text-fig. 20*c*′) lacks any remains of the osseous content, but the lateral lamina is represented by a bony bridge which may be fenestrated (Pl. 37). The pterygoid hamuli are very wide, meeting in the middle line. They are fully excavated although not greatly inflated.

The 5th nerve branch on exit from the cranium lies within a short bony infundibulum formed by the alisphenoid.

Lagenorhynchus acutus (Text-fig. 20*d* and Pl. 39) differs very little in the distribution of air spaces from *L. albirostris*. A bony portion of the ventral lamina of the pre-orbital extension of the pterygoid persists, in this resembling the condition found in individual specimens of *Pseudorca crassidens*. The ventral extent of the palatine is even more restricted than in *L. albirostris*. The alisphenoid is more attenuated, and presents a much thinner surface laterally than in *L. albirostris*, indicating a greater lateral extension of the pterygoid sac. There is no apparent trace of a bony lateral lamina (Text-fig. 20*d*′). The bony infundibulum associated with the 5th nerve branch is much larger than in *L. albirostris* and almost touches the falciform process.

In *L. obscurus* (Text-fig. 20*e* and Pl. 40) the post-orbital lobe of the sinus projects anteriorly to a greater extent than in either of the two previously mentioned species and probably unites with the anterior lobe. The bony ridge on the ventral surface of the orbital process of the frontal is a very narrow crest. The pre-orbital lobe also shows an anterior extension under the ventral surface of the rostrum.

A small bony fragment of the superior lamina remains under the optic infundibulum. The lateral aspect of the alisphenoid (in the post-temporal fossa) is more extensive than in *L. acutus* but less than in *L. albirostris*.

The osseous lateral lamina of the pterygoid is wanting, as in *L. acutus*, and the alisphenoidal infundibulum of the 5th nerve is much shorter than in either of the previous species (Text-fig. 20*e*′).

The three species of *Lagenorhynchus* show a progressive development of a mesial excavation of the frontal by the post-orbital pterygoid lobe (not shown in figures). The excavation is present in *L. albirostris* as an ill-defined shallow depression lateral to the orbito-sphenoid. It is deeper and better defined in *L. acutus* and attains its maximum development in *L. obscurus* in which its mesial extremity is dorsal to the orbito-sphenoid.

In the genus *Grampus* (Text-figs. 21*a* and 25 and Pls. 41 and 42) the post-orbital and pre-orbital lobes are very much expanded laterally, the anterior sac of the pre-orbital lobe projecting onto the ventral surface of the rostrum.

The post-orbital lobe has a considerable extension posteriorly under the ventral surface of the frontal. The two lobes are in close apposition above the optic infundibulum and appear in some instances to coalesce. The alisphenoid is completely covered by the pterygoid sac and its lateral aspect in the post-temporal fossa is very much reduced. Two posteriorly projecting lobes of the sac in the sphenoidal region surround the 5th nerve branch exit in addition to the anteriorly projecting lobe of the peribullary sinus (Text-fig. 21*a*′).

The palatines (PAL) may or may not be overridden by the pterygoids (PT), in some specimens each palatine is divided by the forward extension of the pterygoid whilst in others a continuous band of palatine lies anterior to the pterygoid.

In the orbito-sphenoidal region part of the osseous content of the superior lamina of the pterygoid remains, but at the level of the foramen ovale no part. The pterygoid hamuli are widely excavated and dilated (Text-fig. 21*a*′).

In *Tursiops* (Text-fig. 21*b* and Pl. 43 and 44) the pre-orbital and post-orbital lobes are merged above the optic infundibulum ; if any separation of the two exists it must be very thin and membranous. The pre-orbital lobe is extended below the maxilla as a well-defined anterior sinus. As in *Grampus* two posteriorly projecting extensions of the sphenoidal portion of the pterygoid sac surround the exit of the 5th nerve branch. Laterally in the same region the whole of the alisphenoid is covered by the sac, the lateral edge of which projects beyond the lateral limit of the bone.

The dorsal lamina in the sphenoidal region (Text-fig. 21*b*′) has no osseous content but in the orbito-sphenoidal region a very small remnant persists. The hamuli are fully excavated but the lateral and mesial laminae are in close proximity.

Stenella (Text-fig. 21*c* and Pl. 45) closely resembles *Tursiops* in the general distribution of the air sac system. The pre-orbital and post-orbital lobes have a dorsal development resulting in the formation of a narrow ridge on the ventral aspect of the frontal (cf. *Lagenorhynchus obscurus*, see above. The pterygoid hamuli (Text-fig. 21*c*′) are rather more dilated than in *Tursiops*.

Delphinus in its turn is closely similar to *Stenella* except that the anterior sac extends very much further anteriorly below the maxilla (Text-figs. 21*d*, *d*′ and Pls. 46 and 47). The pterygoid hamuli are less dilated than those of *Stenella*.

The air sinus systems of the Delphininae dissociated from the bones of the skull are shown in Text-fig. 25 *a–f*.

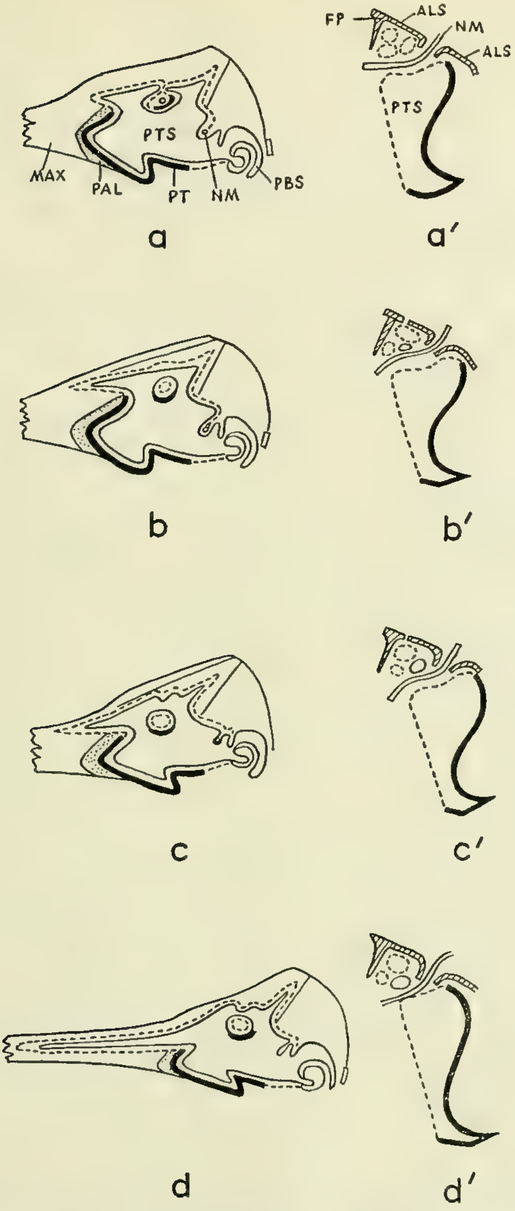
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Fig. 21. Schematic diagrams showing invasion, distention and resorption of the pterygoid bone by the pterygoid sinus in *a* (longitudinal section), *a′* (transverse section), *Grampus*; b, b′ *Tursiops*; c, c′ *Stenella*; d, d′ *Delphinus*.

In *Steno* (Text-fig. 18*a* and Pl. 24) the pre-orbital and post-orbital lobes of the pterygoid sac are well developed and apparently coalesce above the optic infundibulum. As in *Delphinus*, *Stenella* and *Lagenorhynchus obscurus*, there is a conspicuous dorsal development of the pre-orbital and post-orbital lobes, forming deep cavities on the ventral surface of the maxilla and frontal bone which are separated by a smooth, obliquely antero-laterally directed ridge. There is a conspicuous anterior sinus. More posteriorly the sinus system is not so well developed. Thus a considerable portion of the alisphenoid (ALS) remains uncovered and the peribullary sinus does not project very far forward.

A considerable portion of the superior bony lamina of the pterygoid persists (Text-fig. 18*a*′) and the 5th nerve branch is invested in a double, bony infundibulum formed internally of alisphenoid (ALS) and externally of the superior lamina of the pterygoid. The pterygoid hamuli are fully excavated but not dilated, and they are in contact in the middle line.

The supra-orbital process of the frontal of *Sousa* (Text-fig. 18*b* and Pl. 25) is much narrower antero-posteriorly than in *Steno* and correspondingly the excavation of its ventral surface by the pre-orbital lobe is much smaller. The post-orbital lobe is rather more developed and extends high up on the posterior face of the frontal (in the temporal fossa), which is resorbed to the extent that the maxilla is exposed. The lateral expansion of the pterygoid sac in the alisphenoidal region is only moderate, so that a fair portion of the alisphenoid is exposed laterally. The peribullary sinus does not extend far forward.

In the specimen examined (No. 1914.1.14.1) a very minute fragment of the osseous lateral lamina remains in the alisphenoidal region but the dorsal lamina is not represented osseously.

The mesial lamina of the pterygoid (Text-fig. 18*b*′) has a deep concavity in its lateral aspect. The hamuli are excavated but not widely dilated and are separated widely in the middle line.

Text-fig. 23*e* and *f* show the air sac system, dissociated from the skull bones, in the Stenidae.

The chart shown in Text-fig. 26 shows a co-ordination of increasing specialization of the sinus system with the orthodox idea of classification of the Cetacea. There are however certain deviations from the conventional classification which will be discussed. The chart demonstrates a normal frequency distribution in the degree of specialization. Thus the majority of forms have a moderately specialized sinus development while the extremes at both ends are represented by fewer forms.

In terrestrial mammals, generally speaking, the pterygoid plate is a single laminar bone, and it is noteworthy that amongst the few exceptions to this rule e.g. *Myrmecophaga*, in which the pterygoid plate is excavated, the latter bone makes contact with the tympanic bulla.

In the Mysticeti, *Caperea* and *Balaena* show approximately the same poorly developed pterygoid sinus. *Eschrichtius* and the balaenopterids are slightly more advanced.

The Ziphiidae sa a family show a remarkable uniformity in the development of the sinus system, a development which, however, is not in the main trend of specialization—being almost wholly associated with the pterygoid hamuli.

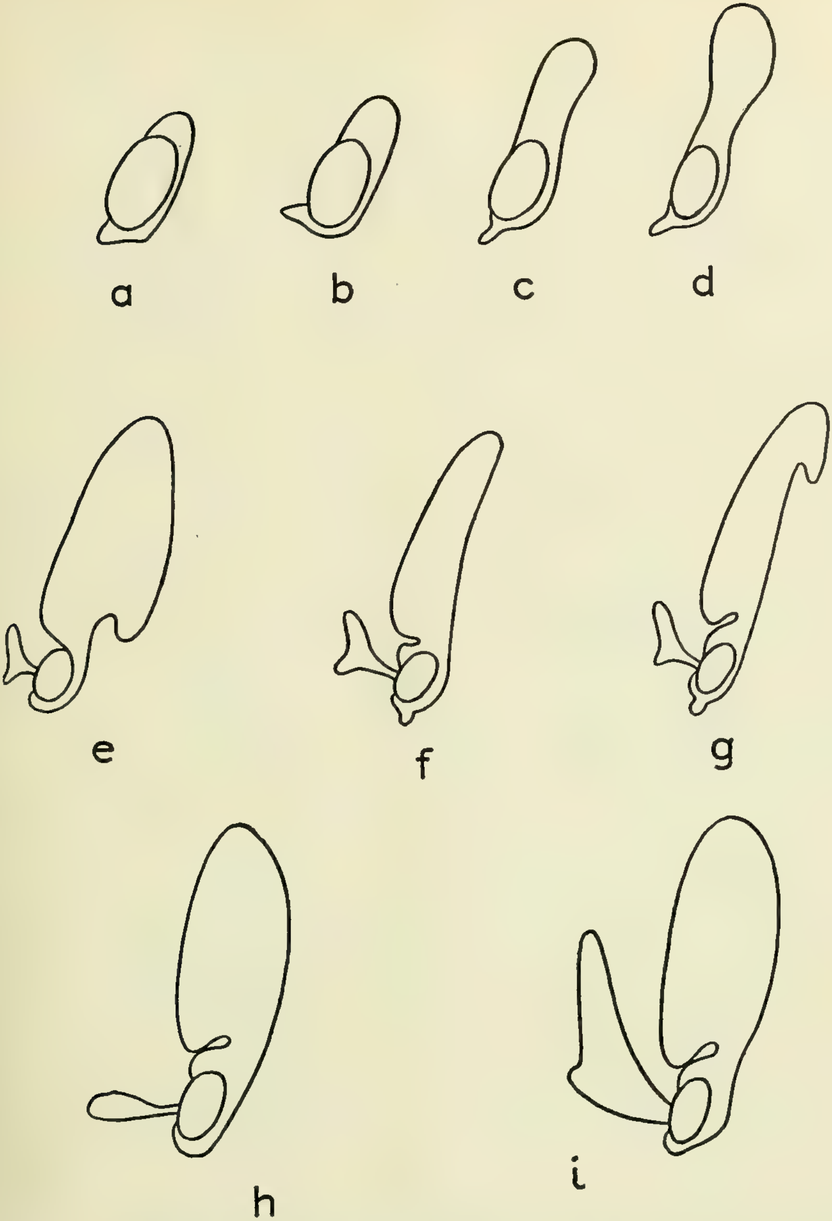

FIG. 22. Diagrams showing progressive distention in the horizontal plane of the air sac system.

a, *Caperea* ; b, *Balaena* ; c, *Eschrichtius* ; d, *Balaenoptera* ; e, *Ziphius* ; f, *Monodon* ; g, *Delphinapterus* ; h, *Kogia* ; i, *Physeter*.

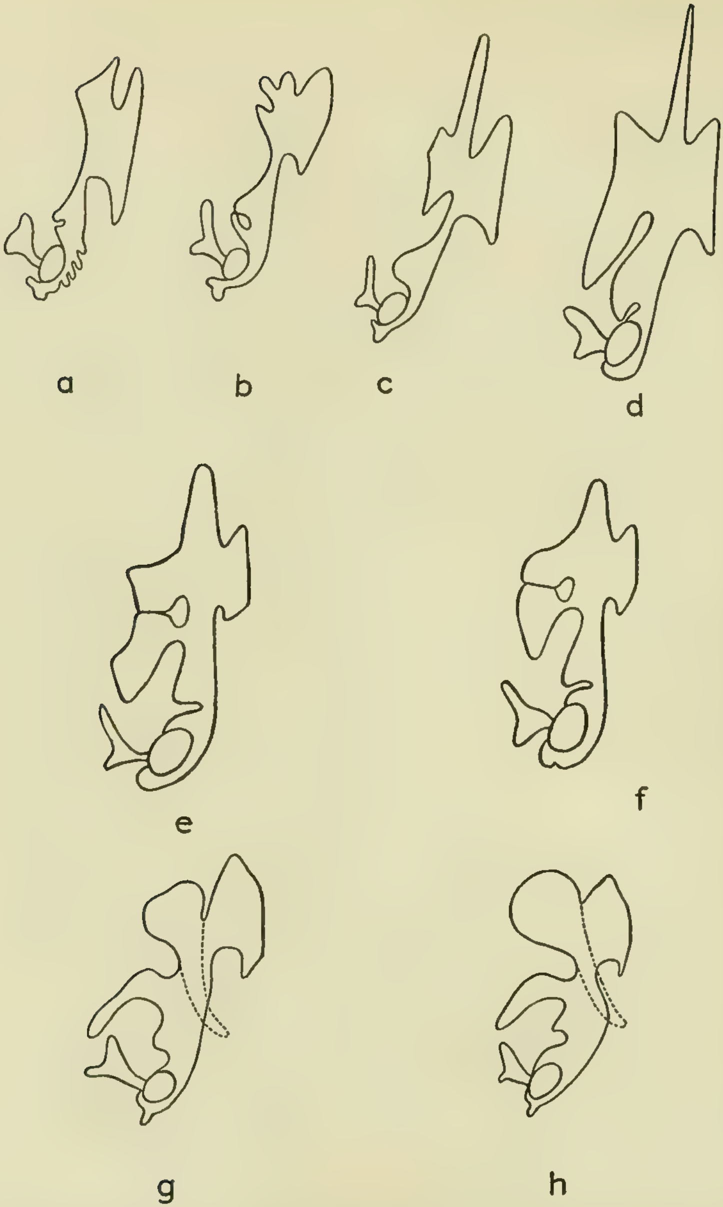

Fig. 23. Diagrams showing progressive distention in the horizontal plane of the air sac system.

a, *Platanista* ; b, *Lissodelphis* ; c, *Inia* ; d, *Lipotes* ; e, *Steno* ; f, *Sousa* ; g, *Phocaena* ; h, *Neomeris*.

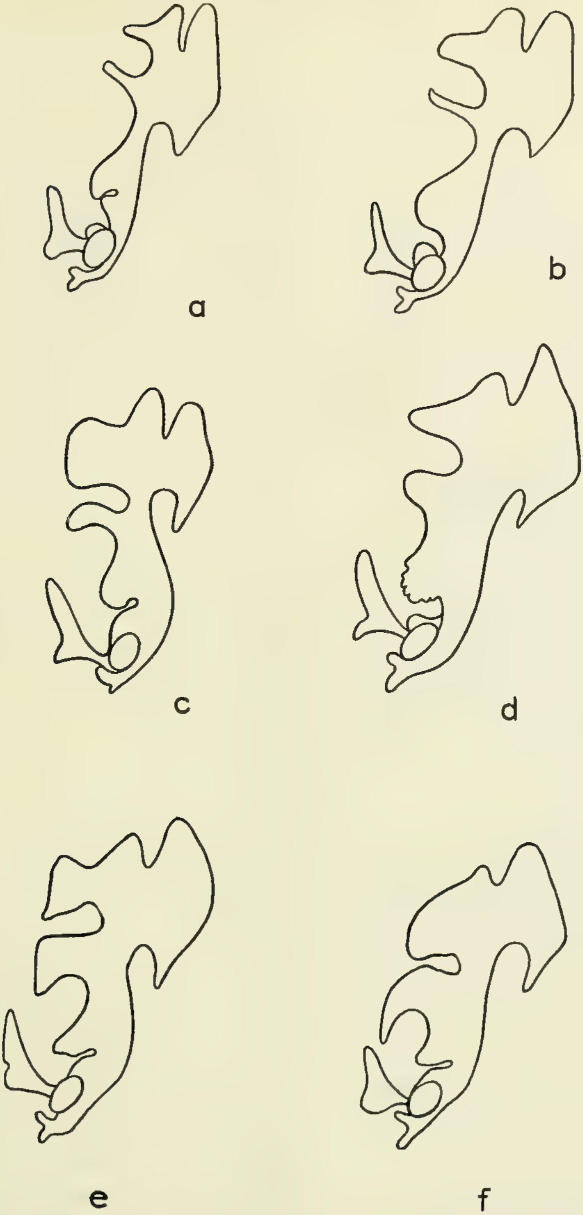

FIG. 24. Diagrams showing progressive distention in the horizontal plane of the air sac system.

a, *Pseudorca*; b, *Orcinus*; c, *Orcaella*; d, *Globicephala*; e, *Feresa*; f, *Cephalorhynchus*.

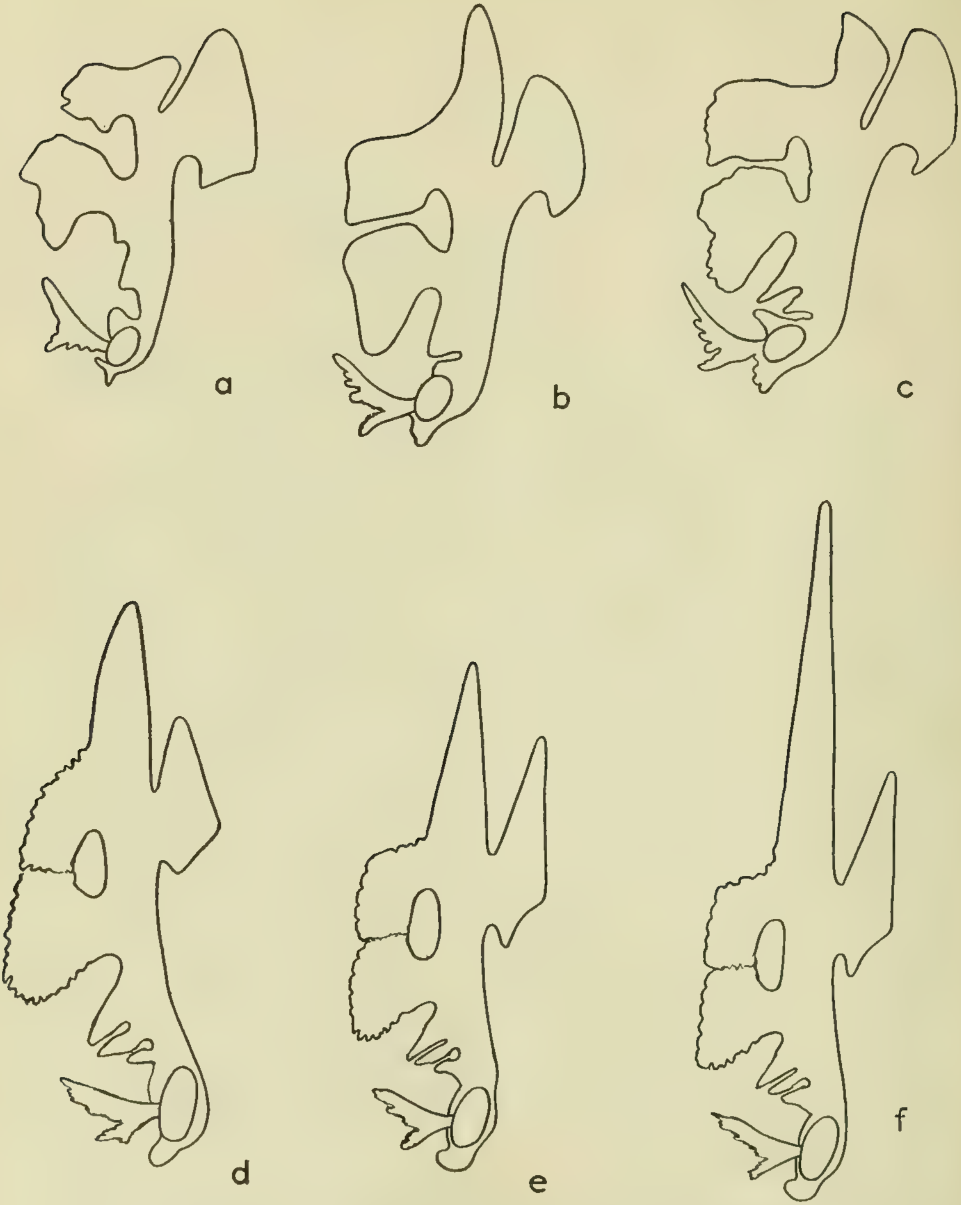

FIG. 25. Diagrams showing progressive distention in the horizontal plane of the air sac system.

a, *Lagenorhynchus albirostris*; b, *L. obscurus*; c, *Grampus*; d, *Tursiops*; e, *Stenella*; f, *Delphinus*.

In respect of the sinus system, the Monodontidae show a primitiveness which justifies the position in which they have been placed in the chart. Slijper (1936), for other reasons, distinguishes the Monodontidae by family ranking, but in respect of the pterygoid sinus system the removal of the family from the Delphinoidea and the creation of a separate super-family in which to include *Monodon* and *Delphinapterus* seems justified.

The Physteridae in some respects resemble the Monodontidae, e.g. in the limited enlargement of the pterygoid hamuli, but in other respects the former are considerably more advanced, there being no trace of superior or lateral laminae.

The Platanistidae, as represented by the four extant genera *Platanista*, *Stenodelphis*, *Lipotes* and *Inia*, cover nearly as wide a range of specialization of the sinus system as encountered in the whole of the rest of the Odontoceti as a sub-order. In this family *Platanista* itself is a mosaic of extremely primitive development and of a specialization encountered nowhere else in the Cetacea. The apparent extension of pneumatization to the maxillary crests is unique, and indeed, may be associated with the under-developed state of the sinus system in the pterygoid region.

Slijper's (1936) opinion about the primitiveness of *Sousa* and *Steno* presents a problem so far as air sinus development is concerned. In this they show a combination of primitive and highly specialized features. Thus in the sphenoidal region the development is poor and can be associated with the relatively large size of the temporal muscles. In the pre-orbital region there is evidence of the development having reached a stage comparable with that of *Tursiops*. In the chart they have accordingly been placed after the Platanistidae and before any of the remaining Delphinoidea.

The distinctness of the Phocaenidae, recognized in Slijper's classification, is supported in the sinus development by the presence, characteristic of this family, of an extension of the pre-orbital lobe into a vacuity between the maxillary and the frontal ; also in the unusual formation of the sphenoidal part of the sinus. For the rest they are rather more advanced than some of the Delphinidae, notably *Pseudorca*.

In the Orcinae, *Pseudorca*, *Orcinus* and *Orcaella* fall into a natural sequence of specialization. So far as *Pseudorca* itself is concerned it is found that considerable individual variation occurs ; thus there are some individuals with a more or less complete bony sheath covering the sinus system, whereas in others all trace of the lateral portions of this sheath has disappeared. In *Orcaella*, an incipient extension of the pre-orbital lobe between the frontal and maxillary is reminiscent of the development in this region, just mentioned as occurring in the Phocaenidae. *Globicephala* and *Feresa* show a general similarity to *Orcinus*, but the development of the pre- and post-orbital lobes is much greater, and in this respect *Feresa* is more advanced than *Globicephala*.

Skull features other than those related to the sinus system would point to *Lissodelphis* being comparatively unspecialized and to be placed in the neighbourhood of the Stenidae. The cranium is low, the backward extension of the pre-maxillae round the nares is limited, so that in this region the maxillae are exposed. The pre-maxillae are of equal length, those of the more advanced delphinids being further extended on the right side than on the left. The maxillae in the neighbourhood of the nares are covered by the mesial margins of the pre-maxillae. On the other hand, the reduced size of the post-temporal fossa and the teeth, which are hardly distinguishable from those of *Delphinus*, indicate a contrasting specialization.

In the sinus system also there is a mosaic of primitive and specialized features. Thus there is little lateral expansion of the system in the sphenoidal region and the paroccipital processes are incompletely excavated. There is no extension of the post-orbital lobe under the post-orbital process of the frontal. Anteriorly however, there is evidence of coalescence of the pre- and post-orbital lobes and a well marked anterior sinus, which is correlated with almost complete disappearance of the bony superior lamina of the pterygoid in this region.

A general assessment of the specialization of *Lissodelphis borealis* with regard to the sinus system particularly, but considering also other features of the skull, seems to justify the erection of the sub-family Lissodelphinae, with affinities with the more specialized genera of the Orcinae on the one hand, and the Cephalorhynchinae on the other.

In the genus *Cephalorhynchus* the chief advance in development is in the pre- and post-orbital lobes which are moderately approximated to each other. In addition, the post-orbital lobe has a narrow diverticulum which passes dorso-posteriorly under the post-orbital process of the frontal.

In the remaining genera, included in the Delphininae, there is a gradual augmentation of the sinus development. Within the genus *Lagenorhynchus*, *L. albirostris* still shows a partial bony lamina while *L. obscurus* in the close approximation of the pre- and post-orbital lobes resembles *Stenella*. The air sinus development in *Grampus* closely resembles that of *Tursiops*, and in general there appears to be justification for including it with the Delphininae rather than, as some authors have done, associating it with the Orcinae. *Tursiops*, *Stenella* and *Delphinus* show a progressive development of the anterior sinus which reaches its extreme extension in the last named genus.

The chart thus shows that in the evolutionary development of the sinus system there is an over-all sub-ordinal trend towards greater specialization, but also within the lower ranks of the hierarchy similar trends can be distinguished, even to the specific level in *Lagenorhynchus*.

FUNCTION

The mode of hearing of whales has for long been a subject of controversy among cetologists. Apart from those who maintained that cetaceans are unable to hear water-borne sounds, the most generally accepted hypothesis has been that these animals hear by bone conduction, that is by the perception of vibrations through the skull directly to the cochlea. It is proposed to show that this method of hearing is not only undesirable but also that it is impossible in normal circumstances in the cetaceans.

EXTERNAL AUDITORY MEATUS

In order to substantiate statements which will be made later about the function of the external and middle portions of the ear, it is necessary to review certain features of their anatomy.

	Pterygoid plate complete.	Disappearance of superior lamina in orbital region, partial.	Disappearance of superior lamina in orbital region, complete.	Increased lateral expansion of pre- and post-orbital lobes.	Lateral expansion of sphenoidal part, complete.	Posterior extension of sphenoidal part with encirclement of Vth nerve single & advanced.	Posterior extension of sphenoidal part with encirclement of Vth nerve double & advanced.	Coalescence of pre- and post-orbital lobes above the optic nerve.	Anterior sinus elongated.
Terrestrial Mammal	X								
Mysticeti									
Balaenidae									
Balaeninae									
Caperea									
Balaena									
Eschrichtidae									
Eschrichtinae									
Eschrichtius									

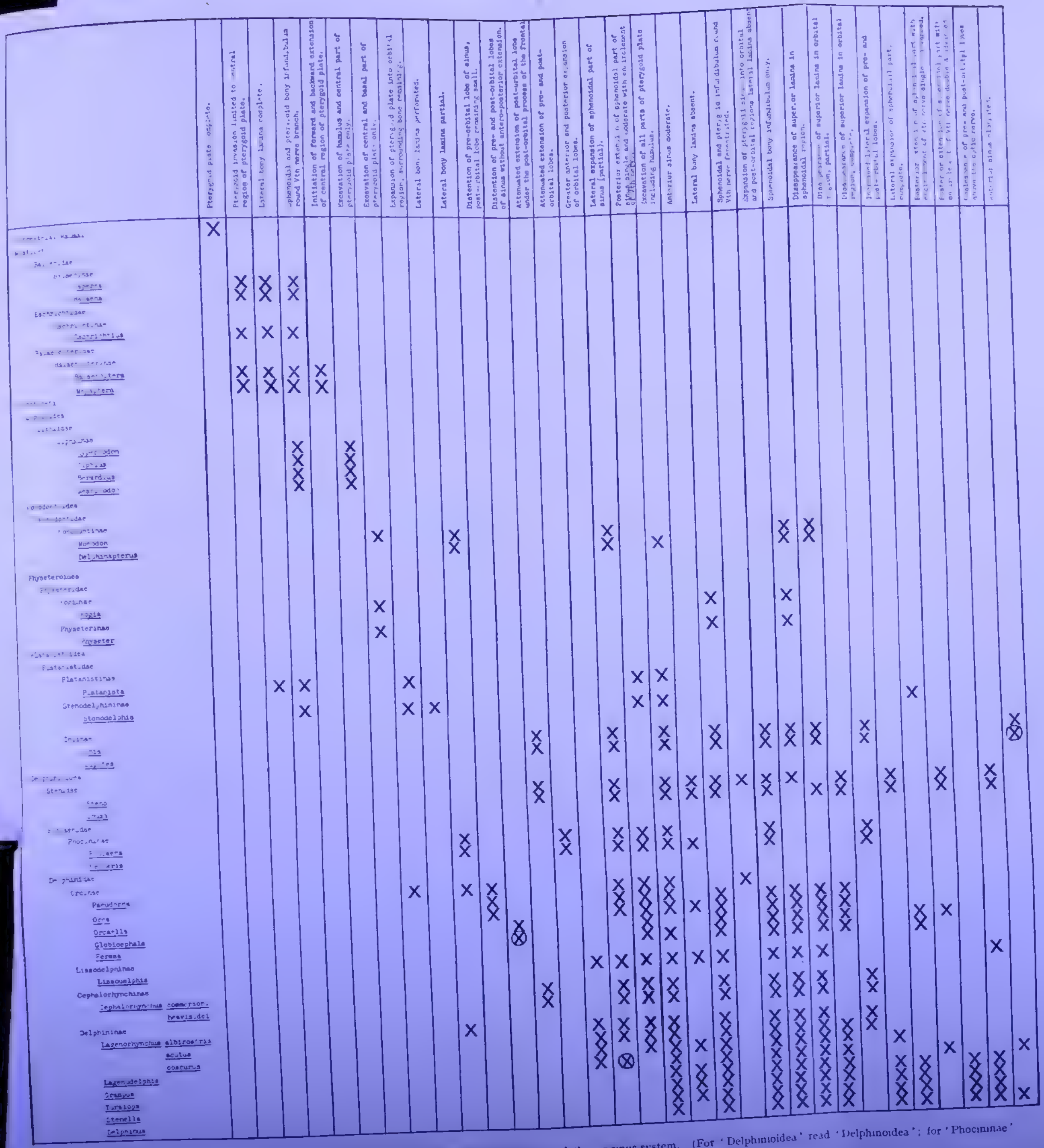

FIG. 26. Chart showing classification of the Cetacea in relation with increasing specialization of the air sinus system. (For 'Delphinioidea' read 'Delphinoidea'; for 'Phocininae' read 'Phocaeninae'; for *Orca* read *Orcinus*. Circles indicate unverified features).

Several descriptions exist of the structure and course of the external auditory meatus in the Cetacea. The absence of an external pinna was noted by some of the earliest writers; Rondelet (1554) appears to have been the first to notice the external aperture of the ear. In the smaller odontocetes it is less than a millimetre in diameter and can only be detected by careful examination of the region behind the eye. The aperture in the larger, baleen whales is lenticular in shape, usually concealed in a groove and measures about 1 cm in its larger diameter.

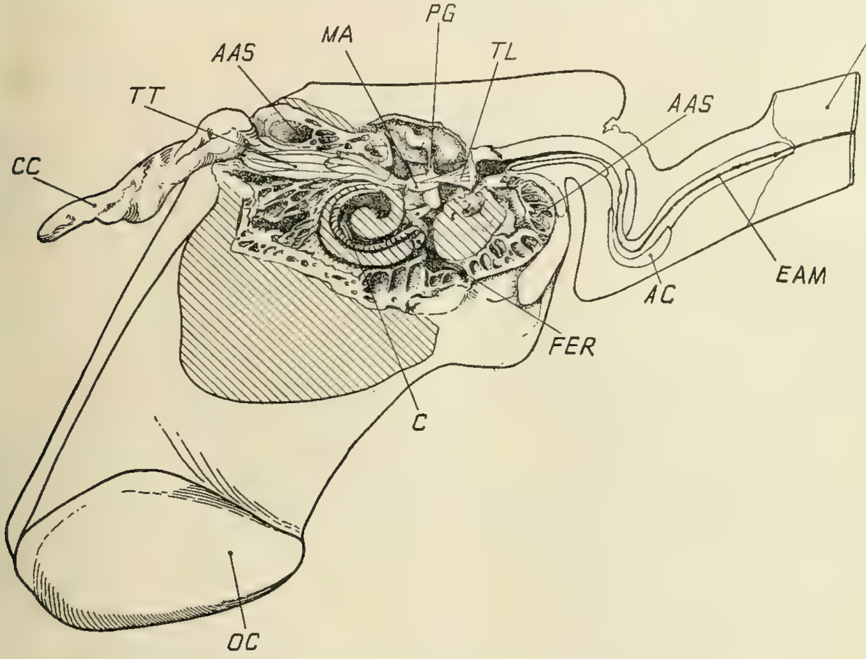

Fig. 27. Diagram of a dissection of the ear of *Globicephala melaena* (cf. Plate 49). Ventral view, left side.

The course of the meatus in *Globicephala melaena* from the surface of the body to the external aspect of the tympanic membrane is shown in Text-fig. 27. The tube (EAM) passes inwards more or less horizontally for about 2·5 cm, then dorsally and caudally in a sharp bend which occupies another 2·5 cm, rounding again to its original direction to its termination at the tympanic membrane. The mean axis of the meatus is at right angles to the long axis of the body.

According to Lillie (1915), in *Megaptera novaeangliae*, from the external orifice " a tube about 1/10 in. in diameter traversed the blubber which was about 3½ in. thick in this region. The tube was continued through the underlying tissue for about 2 in. and gradually decreased in diameter until it ended blindly. The meatus was closed up for about 3 in. of its course It widened out again to a diameter of rather more than an inch and maintained a more or less uniform size for the remainder of its passage to the tympanic bulla. The total length of the canal was about 1 ft. 9 in. in a humpback whale 40 ft. in length. The walls of the wide innermost portion were invariably pressed together." Lillie pointed out that Burfeld & Hamilton noticed that in several of the *Balaenoptera* examined by them the meatus was closed up for part of its course. This was further confirmed by the present writers during the dissection of a Fin Whale, *Balaenoptera physalus*, the closed portion of the meatus being partially invested in cartilage (see Pl. 51).

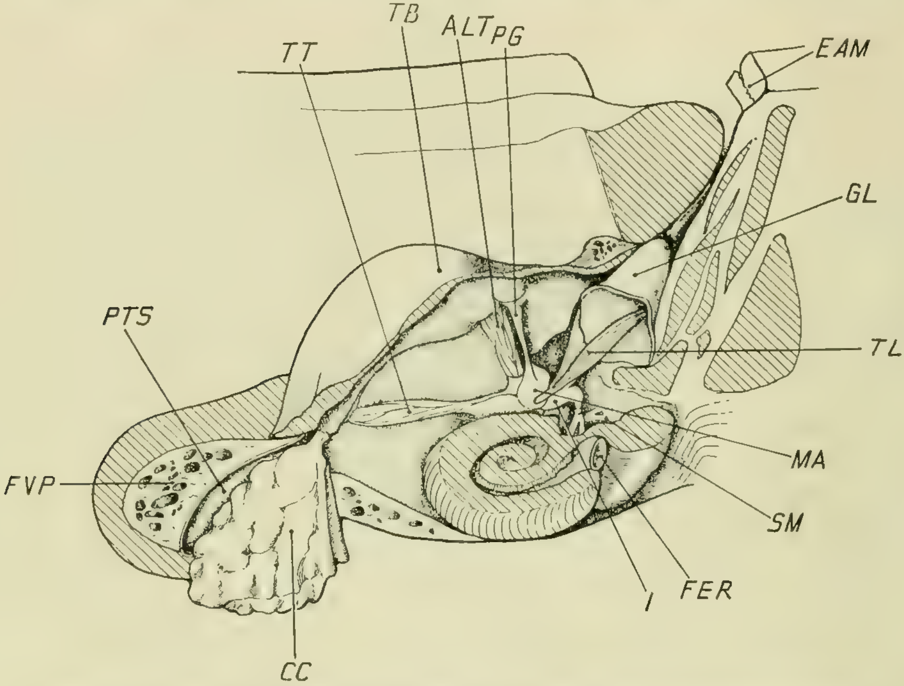

FIG. 28. Diagram of a dissection of the ear of a juvenile *Balaenoptera acutorostrata* (cf. Plate 50). Ventral view, left side.

Carte & MacAllister (1867) reported that in *B. acutorostrata* the meatus was open. In the foetal specimen of *B. acutorostrata* dissected in this museum (Text-fig. 28) the meatus (EAM) appeared to be closed about $\frac{3}{4}$ in. from the external aperture but a section through the apparently closed portion (see Purves 1955) shows that a minute perforation exists.

In a foetal specimen of *Megaptera* sectioned and kindly lent by Professor D. V. Davies, St. Thomas' Hospital Medical School, it was noted that the external open portion was very shallow (Pl. 48*a*), perhaps because of the absence of a thick blubber layer. Internal to this opening was a closed portion (Pl. 48*b*) followed in its turn by an open tube, which soon became occluded for a short distance before opening out again in the innermost portion ending in the tympanic membrane (TM) (Pl. 48*c*).

In the Sperm Whale, Clarke (1948) describes the external auditory meatus as commencing as " a short blind sac which penetrates from the auditory aperture for a distance no deeper than the blubber thickness. The sac has somewhat thickened unpigmented walls. . . . Internally these walls are thrown into transverse folds. . . . Dissection reveals that the proximal portion running in the temporal bone is still intact. Also in two physically immature adults the external meatus after termination of its cavity was prolonged into a short solid stick representing the canal after obliteration of its lumen." Yamada (1953) also notes the presence of a solid cord beneath the blubber layer and could not demonstrate any lumen in it. In a specimen examined by the present writers, the apparently solid cord contained a number of small, spherical cavities lined by pigmented epidermis separated by short intervals in which no lumen could be detected.

More or less detailed descriptions of the structure of the meatus have been given by such writers as Carte & MacAlister (1868), Buchanan (1828), Hanke (1914), Yamada (1953) and Ryseenbach de Haan (1957). In general it appears that, as described by Carte & MacAlister, there are three layers forming the wall of the meatus. Lining the tube is an involution of the cuticle, this is usually pigmented, and in the specimen of *G. melaena* dissected (Text-fig. 27) it is of a dense black colour throughout its length. The cuticle is enveloped by a thick, rigid, fibrous, middle layer and external to this again a fibro-cellular layer, in which, according to Carte & MacAlister, a thin stratum of circular constrictor muscle is present.

Elastic fibro-cartilaginous masses are associated with the wall of the meatus in all those odontocetes which have been examined. In the mysticetes, Hanke (1914) says that the cartilage is absent but Carte & MacAlister (1868) and Boas (1912) have described, and the latter has figured, a cartilaginous mass associated with the meatus of *B. acutorostrata*. It has also been found in a recently dissected specimen of Fin Whale (see p. 135 and Pl. 51). It is suggested by the present writers that Buchanan's (1828) " globular substance " in *Balaena mysticetus* may in fact be the ear cartilage. In the Odontoceti the cartilage is more extensive than in the Mysticeti (*B. acutorostrata*). Its position and shape in *Phocaena phocoena* and *Lagenorhynchus acutus* are figured by Boas in his pls. 12 and 25.

The cartilage is also evident in the specimen of *G. melaena* dissected in this Museum (Text-fig. 27, AC). It occupies much the same position as that figured for *Ph. phocoena*. The more reduced condition of the cartilage in *B. acutorostrata* is indicated in Boas' figure.

Boenninghaus (1903) compared the ear cartilages in the Odontoceti with those of seals, and came to the conclusion that the former showed a further stage in the process of retraction of the pinna to that exhibited in seals, in which the pinna is withdrawn inside the meatus prior to submergence. Boenninghaus argued that the absence of external pinna in the cetaceans was correlated with their purely aquatic mode of life. Boas' paper on the ear cartilages of mammals (1912) supports this point of view.

Vestigial outer ear muscles have been described by Boenninghaus (1903) (see Pl. 1, fig. D), Beauregard (1894) and Hanke (1914), the last discussing their homologies in detail and producing a comparative table of his own and other workers' conclusions. Hanke (p. 303) cites the presence of sweat glands in the meatus of the baleen whales and suggests, from the absence of sebaceous glands, that the plug in contact with the " glove finger " of the tympanum is not a true ear wax but a secretion similar to this. However it is generally accepted that the glands producing ear wax in man are modified sweat glands and there appears to be no reason why this should not apply to the Cetacea also. Carte & MacAlister described " a very distinct series of ceruminous glands the orifices of whose ducts were visible in the lining membrane ".

A characteristic feature of the external meatus of the rorquals and the Humpback is the elongated plug of wax and desquamated epithelium which caps the " glove-finger " extension of the tympanic cavity. Typically this is an elongated, roughly conical mass, brownish in colour, scored longitudinally by numerous shallow grooves and flattened dorso-ventrally throughout its length. It fills the meatal cavity mesial to its blind portion. The base of the cone is occupied by a rounded, conical concavity which fits onto the distal end of the " glove-finger ". The homologies of the " wax-plug " are indicated by Purves (1955).

Buchanan's (1828) description of the meatus in the Greenland Right Whale (*Balaena mysticetus*) indicates that in this species the lumen is continuous throughout its course. Buchanan's particular interest was in the ceruminous secretion of the ear and he describes it as being of a greyish-blue colour and in no great quantity.

The evidence from the Delphinidae is that the lumen of the meatus is continuously open from the exterior to the tympanic membrane. From this it may be assumed that the presence of the ear-plug in the rorquals and Humpback is a direct result of the closure of the meatus along part of its length. The absence of an ear-plug in the Sperm Whale has yet to be confirmed.

TYMPANIC MEMBRANE

Hunter (1787) gives a brief description of the tympanic membranes of Toothed and Baleen Whales, and Buchanan (1828) describes the membrane of *Balaena mysticetus* and *Monodon monoceros*. Of more recent descriptions of this structure in odontocetes, those of Beauregard (1894) and Boenninghaus (1903) coincide in a general way with the condition found in the specimen of *Globicephala melaena* examined by the present writers (Text-fig. 27, TL and Pl. 49).

The general shape of the Narwhal tympanic membrane was described by Buchanan as comparable with a convolvulus flower in having an oval, concave, exterior surface and, within the tympanum, a core tapering to a very attenuated attachment on the malleus. The condition in the recently examined *Globicephala melaena* is more in agreement with Boenninghaus' description of what he found in *Phocaena phocoena*. Thus the external aspect of the tympanic membrane is more shallowly concave than funnel-shaped. Hyrtl's (1845) description of the tympanic membrane of the Narwhal disagrees with Buchanan's. In this species, as in the Bottlenosed Dolphin, he describes the membrane as presenting externally not a single, but a double concavity in the form of two pits separated by the rectilinear base or origin of the extension of the tympanic membrane to the malleus. In the recently examined *Globicephala* neither trace of the rectilinear base of Hyrtl, nor of the linear depression described by Beauregard, could be detected. In *G. melaena* the internal extension of the tympanic membrane to the malleus is not centrally placed in relation to the external concavity, but displaced towards the posterior margin of the tympanic annulus, so that anterior to the extension there is an incipient depression on the internal face. This condition corresponds to that in the Common Porpoise described and figured by Boenninghaus. The internally extending " fleshy process " of the tympanic membrane is flattened, triangular and elongated, its apex being attached to the malleus (Text-fig. 27, MA). The flattening is obliquely antero-posterior so that the ventral margin of the process is slightly in advance of the dorsal.

The meatal aspect of the " membrane " is covered by a densely black epithelium continuous with that of the external auditory meatus. In the specimen dissected, the coarse, fibrous structure of the extension to the malleus can easily be seen with the naked eye (Pl. 47). The bundles of fibres spring from a very narrow attachment on the small tubercle of the malleus, and diverge in straight lines in their course to the tympanic annulus. On the anterior aspect these fibres extend almost to the same extent as do those on the posterior aspect. As the fleshy process is not centrally placed, there is an interval between the outward termination of the fibres and the anterior margin of the tympanic annulus which is closed by the mucous membrane of the tympanum internally, and by the epithelium of the external meatus externally. Boenninghaus found that in *Phocaena phocoena* the drum membrane had irregular areas of fibreless tissue, anteriorly between which the fibres continued to bony prongs on the annulus. In *G. melaena* the separation of the fibres from the anterior margin of the annulus is more complete so that a much larger fibreless region is present, reminiscent of the *pars flaccida* of the human tympanic membrane.

Boenninghaus saw both radial and circular fibres and made the significant statement "all the radial fibres continued into the spur and the latter owes its solidarity to their thickness and stiffness. The circular filaments proceed fairly high up the spur. *All in all the spur is nothing less than the extended centre of the drum.*"

As with the Odontoceti, so with the Mysticeti, the characteristic tympanic membrane has attracted the attention of such workers as Hunter (1787), Carte & MacAlister (1868), Beauregard (1894), Hanke (1914), Lillie (1915) and Kernan (in Schulte 1916) who concentrated on the rorquals. Home (1812) and Buchanan (1828) described the tympanic membrane of the Greenland Right Whale.

Lillie employs the similarity of the membrane to a glove finger when describing it. In his specimen the walls of the sac were 1/10 in. in thickness and consisted chiefly of white fibres and yellow elastic tissue. There was no evidence of nerve cells, nerve fibres or muscle fibres in the tissue. " From the upper surface of the sac, in the median line, a ligament about an inch long and 5 mm in diameter projects towards the tympanic cavity. The ligament is continued along the sac in the opposite direction as a ridge. . . . The mouth of the sac opens into the tympanic cavity while the outer portion projects into the external auditory meatus. The ligamentous process passes under the junction of the malleus and incus and becomes attached at its proximal end to the very much reduced manubrium of the malleus."

A re-description of the tympanic membrane in the light of the evidence furnished by a recently dissected *Balaenoptera acutorostrata* specimen (Text-fig. 28 and Pl. 50), and a re-examination and further description of Lillie's specimen of *Megaptera novaeangliae* is required. Fundamentally the tympanic membranes in these two specimens are similar.

From its attachment on the manubrium of the malleus (MA) the ligament (TL) extends in the direction of the external meatus (EAM) as a broad band which widens perceptibly as it proceeds outwards. The posterior half of the band is much stouter than the anterior, and it is the posterior portion which continues into the glove finger for about one third of the latter's length. None of the fibres of the posterior portion of the ligament is attached to the tympanic annulus; a deep, tapering concavity penetrates into its fibres from its outer, meatal surface. The tympanic membrane as a whole is thus composed of two distinct parts, (1) a fibrous portion with an external concavity and (2) a non-fibrous portion which projects into the external auditory meatus. The fibrous portion is exactly similar to, and comparable with, the so-called triangular ligament found in the Odontoceti, while the glove finger represents a greatly enlarged development of the fibreless region mentioned above in the descriptions of *Globicephala* and *Phocaena*, and represents a further dissociation of the fibrous portion of the tympanic membrane from the tympanic annulus.

Beauregard (1894) homologizes the glove finger with one of the accessory air sacs—the sac moyen. This is referred to on page 10 *supra*.

The description and figures of Home (1812) and Buchanan (1828) of the tympanic membrane of the Balaenidae, as exemplified by *B. mysticetus*, make possible a close comparison with this region in the Balaenopteridae. Thus the hemispherical extension into the external meatus can be identified with the glove-finger, and the so-called valvular process of Buchanan corresponds with the fibrous portion found in the balaenopterids. From Home's figure it would appear that the fibrous portion has a more extensive attachment to the tympanic annulus than exists in the balaenopterids; this characteristic, together with the broad triangular shape of the fibrous portion of the membrane extending to the malleus, is related to the more limited extension of the glove finger into the external auditory meatus. The general construction of the tympanic membrane in the Balaenidae is intermediate between that of the Odontoceti and the Balaenopteridae. Incidentally, with reference to the membrane of *B. mysticetus*, Knox (1859) corrected the erroneous impression of Buchanan that it was muscular.

Ridewood's (1922) description of the skulls of foetal Humpbacks and rorquals includes accounts of the developmental appearance of the tympanic membrane. He discusses comprehensively the interpretations of earlier workers, including particularly those of Hanke, Beauregard & Lillie. His references briefly summarized are as follows. In a 6-in. foetus of *Megaptera* the tympanic membrane is still flat and horizontal in position, forming part of the roof of the inner end of the external auditory meatus. He states that the membrane is supported on three sides, anterior, mesial and posterior, by the tympanic annulus and that its outer edge passes into a mass of fibrous tissue attached to the lower edge of the squamosal bone. He draws attention to a pale streak on the area referred to by him as the tympanic membrane (his fig. 4, p. 223), and states that it marks a tract of fibrous tissue " to the mesial end of which the extremity of the manubrium mallei is attached, it is this fibrous tissue that develops later into the long conical ligament of the adult tympanic membrane ". Further on in this paper (p. 244) Ridewood states that " there seems to be no question that the thimble-shaped membrane of the 27-in. foetus, and presumably the glove-finger membrane of the adult whale, represents the whole of the tympanic membrane." This view is not held by Beauregard, Hanke or the present writers.

Considering first the boundaries of the tympanic membrane as mentioned above, the sagittal sections of Prof. Davies' 6-in. Humpback foetus indicate that Ridewood set too wide a limit to the extent of the membrane. The tympanic membrane occupies less than a half of the area within the tympanic annulus, in a position corresponding to the pale streak to which Ridewood refers. The relation of the tympanic membrane (TM) both to the external meatus (EAM) and to the manubrium mallei (MM) are clearly shown in the section (Pl. 48*c*). The external face of the membrane forms a deeply concave, conical depression on the roof of the external auditory meatus and is comparable in shape with the tympanic membrane of the adult odontocete.

Ridewood's interpretation of the glove-finger of the adult as the whole of the tympanic membrane is at variance with the present writers' conclusions. As already stated the tympanic membrane is represented by the fibrous ligament *and* the glove finger and not by the glove finger alone. In this connection it may be pointed out that, in the 6-in. foetus (Davies' specimen), while the tympanic membrane is still horizontal in position, it is already divisible into two parts. Firstly, the portion already described and shown in Pl. 48*c*, and, secondly, Pl. 48*d* shows that the external meatus continues beyond the limit of the manubrium mallei and is roofed over by a portion of the tympanic membrane which is flat, and apparently lacking distinct fibrous structure. It is from this portion that the present writers believe that the glove finger is developed.

MIDDLE EAR

As in the Mammalia generally, the chain of auditory ossicles is composed of three elements. Numerous descriptions exist of their form in the Cetacea (Camper, Hyrtl, Beauregard, Carte & MacAlister, Boenninghaus, Yamada, Reysenbach de Haan). It is therefore not proposed here to give a detailed description but to refer to those aspects of their construction which do not appear to have been mentioned previously. A general impression of their shape and arrangement is shown in Text-figs. 27–29.

The fusion of the processus gracilis of the malleus (PG) with the tympanic bulla (TB) is frequently considered to be peculiar to cetaceans but, according to Boenninghaus this condition is fairly common in other mammals. He says " it is always fused (to the tympanic ring) at the Glasserian fissure in the newly born human. In man however, and in many (other) mammals, the fusion later dissolves and the connection disappears. In other beasts the connection continues throughout life. Hyrtl includes monkeys, carnivores and insectivores and, mistakenly, man. I had the opportunity to examine these connections in the lion and hedgehog and it really is a bony growth." Boenninghaus goes on to contrast the stoutness of the processus gracilis of the malleus in whales with its slenderness in other mammals, but it should be pointed out that in the Cetacea generally, while the process is indeed stout in forms such as the rorquals and Humpback it is of much more slender construction in the Right Whales. Again, in the odontocetes, while the attachment of the process to the tympanic ring is elongated its thickness is very greatly reduced. The attachment in *Phocaena phocoena* is so attenuated that, with the exception of Boenninghaus, authors have described it as being unfused.

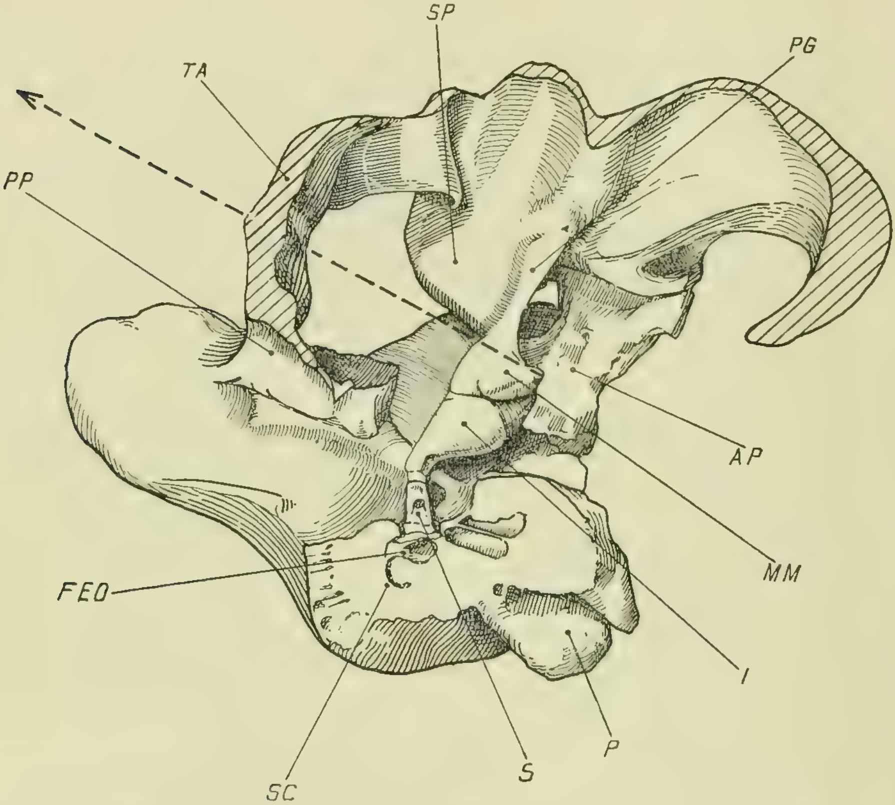

FIG. 29. Right tympanic annulus and auditory ossicles of a Humpback Whale, *Megaptera novaeangliae*. The dotted line indicates the long axis of the tympanic ligament.

MALLEUS

(a) *Anterior process.* For the later consideration of the functioning of the malleus, it is necessary to describe, in some detail, aspects of its structure not previously emphasized. Starting with the processus gracilis (PG) it will be seen from the figure of its anterior aspect (Text-fig. 29), that it is closely associated with the sigmoid process (SP) of the tympanic bulla (TB) which forms a buttress attached to about four fifths of its lateral border. The mesial border of the process is free from any attachment throughout its length. Between these two borders, which are thickened, is a roughly rectangular area of much thinner bone, the borders and the thinner portion forming what may be described as a channel girder. In posterior view the process forms the convexity of the girder, and it will be seen from Text-fig. 29 that this surface is fused to the sigmoid process at a deeply grooved, arcuate junction extending from the meso-ventral to the dorso-lateral edge of the process. Examination of the junction in strong light shows that the dorso-lateral part of it is translucent, the bone in the region being extremely thin, even in the adult rorqual. In general construction the odontocete processus gracilis is essentially similar to that just described for the rorqual except that the concavity of the " girder " is not so emphasized.

(b) *Manubrium.* Unlike the typical, handle-shaped manubrium of most mammals, including man, that of cetaceans is short, stout and roughly conical (Mysticeti) (Text-fig. 29) or globular (Odontoceti) in form (Pl. 49). Its mass is comparable with that of the head of the malleus. At the lateral end of the inferior surface in the Mysticeti, a small promontory is identified as the short process (processus brevis). In the Odontoceti a small pointed process, directed towards the head, and situated about midway along the length of the lower surface of the manubrium, has been identified by Hyrtl as the short process. In the Mysticeti the attachment of the tympanic membrane to the malleus extends to the whole length of the posterior face of the manubrium, whereas in the Odontoceti this attachment is restricted to the short process. On the proximal edge of the anterior aspect of the manubrium a small tubercle forms the point of attachment of the tensor tympani muscle (Text-figs. 27 and 28 TT).

(c) *Head of the malleus.* The massive head of the malleus (Text-fig. 29) is deeply marked by two large facets making a re-entrant angle on its posterior aspect. Both these facets have smoothly convex surfaces covered with articular cartilage, which, with corresponding facets on the incus, form part of a synovial joint. The radii of the convexities, as well as that of the arcuate junction between the two facets, lie approximately at right angles to the long axis of the tympanic ligament (see Text-fig. 34*d*).

INCUS. In general shape the incus (I) is in the form of a short, wide-based cone, the apex of which is curved upwards to end in the facet which articulates with a corresponding facet in the stapes (Text-fig. 29). The base of the cone forms the larger of two facets which articulate with the malleus. The smaller facet is approximately at right angles to the larger on the ventral aspect of the ossicle. For articulation with the malleus, both facets are shallowly concave and their line of junction is also concave. Like the facets of the malleus these also are furnished with articular cartilage. The short process is a short, conical projection directed anteriorly in line with the lateral margin of the processus gracilis of the malleus. The facet for articulation with the stapes is an oval, the long axis of which is parallel to the larger incudo-malleolar facet.

STAPES. The stapes (S) is less obviously stirrup-shaped than in most other mammals and although in the rorqual an intercrural foramen exists, this is not so in all cetaceans. There is no well-defined neck separating the head from the crura and the foot is oval in shape, with a smooth, flanged edge moulded to fit precisely into the fenestra ovalis (FEO). Contrary to what has been stated by many authors the present writers have been unable to find any evidence that the stapes is ankylosed to the fenestra ovalis. It is believed that the impression of fusion is due to the perfect fit of the foot of the stapes in the fenestra ovalis.

MUSCLES OF THE MIDDLE EAR. As Hunter (1787) pointed out, the cetacean tympanum, like that of other mammals, contains two muscles, the tensor tympani and the stapedius (Text-figs. 26 and 27, TT and SM).

In the Odontoceti (*Globicephala melaena*) (Text-fig. 27) the tensor tympani (TT) arises from the dorsal wall of the tympanic cavity near that part which transmits the Eustachian tube. It is attached in a small depression at the tip of the manubrium mallei. Although it is directed approximately in line with the long axis of the tympanic ligament (TL) as viewed ventrally, the two attachments are displaced from each other by about 2 mm when viewed in the lateral aspect. The muscle is intimately associated with the cavernous body (CC) of the tympanic bulla to the extent that Beauregard (1894) regarded the muscle as the attachment of the cavernous body of the malleus.

The stapedial muscle is in the normal position.

The evidence produced by Boenninghaus (1903) and Kolmer (1907), among others who examined the inner ear of cetaceans, is to the effect that the essential organ of hearing, i.e. the cochlea, is comparable in general structure with that of terrestrial mammals. Indeed the essential organ of hearing in certain respects gives indications of being sensitive to a much wider range of frequencies than that of most mammals.

THEORETICAL CONSIDERATIONS AND EXPERIMENTAL EVIDENCE

THE HYDRODYNAMIC FUNCTION OF THE AIR SACS

It has often been asserted that the function of the auditory ossicles is concerned with the matching of the incoming air vibrations with those of the fluid vibrations of the cochlea, and it is on this basis that it has been maintained that there is no necessity for an ossicular system in the Cetacea. The fact is that the Cetacea have a functional chain of ossicles and that the stapes is movable in the oval window. The fenestra rotunda is also functional. This implies that some kind of molar, as distinct from molecular, disturbance of the cochlear fluid is required to produce the sensation of hearing. This again points to the maintenance of an air space in the middle ear. The question of the manner in which this air space persists in spite of the enormous variations in pressure to which it is subjected is directly related to one of the functions of the pterygoid sinuses. Amongst other functions, which will be enumerated later, is that concerned with the regulation of pressure on either side of the "ear drum". In the Cetacea (see above p. 113) the pars flaccida is modified and sometimes greatly enlarged, and the pars tensa drawn out in the form of a ligament, the tension on which appears to be maintained by the internal pressure on the pars flaccida and by the operation of the muscle described on p. 135. In mammals, the pressure in the middle ear cavity is adjusted according to immediate necessities, by increments of air from the respiratory tract, by way of the Eustachian tube. In the Cetacea the only opportunities for effecting an adjustment by this method are when the animal surfaces for breath. It seems likely that the pterygoid air sinuses form a reservoir for this process of pressure regulation, and that the maximum depth to which the animal can dive is in relation to the ultimate compressibility of the air sacs and the size of the tympanic cavity.

It has been stated above (p. 30) that the sinuses and tympanic cavity are filled with a foamed, oil-mucus emulsion so that the compressibility of the air sacs ultimately depends on that of the foam and the rigidity of the surrounding tissues.

The question naturally arises about the persistence of the gas in the foam cavities and the maintenance of acoustic isolation (see p. 121) under great pressures. Experiments were made on the relation to pressure of gelatinous, albuminous and detergent foams. The foam to be investigated was placed in a pressure-tight, optical cell and observed by transmitted light through a vertically mounted, low power microscope with micrometer eyepiece. Pressure was applied by pumping B.P. liquid paraffin into the cell (in direct contact with the foam) and was measured on a Bourdon gauge. As pressure increased above atmospheric, the gelatinous foam bulk volume decreased considerably and the foam structure was replaced by a system of spherical air bubbles dispersed in liquid. These bubbles were a few microns in diameter and separated by distances of comparable magnitude. The system was stable at higher pressures, and the bubbles had not disappeared after 20 minutes at 100 atmospheres. On release of pressure to one atmosphere the foam structure reappeared. Using egg albumen, the foam structure was again replaced by air bubbles, dispersed in a continuous liquid phase, which persisted at 100 atmospheres. The bubbles were of less regular size and shape than in gelatin. Using the detergent, the foam structure collapsed under pressure and no bubbles were visible at higher pressures.

From the results of the experiments just described, and assuming that the naturally-occurring foam behaves in a similar manner to that of gelatinous and albuminous foams, it may be deduced that, even at the greatest depth to which cetaceans normally dive, air bubbles would persist and there would be a sound reflecting system surrounding the essential organ of hearing. Some of the smaller cetaceans are capable of undergoing very rapid changes of depth and are also dependent upon a very acute sense of directional hearing. The rate of change of bulk volume of the foam would be important because of the variation in pressure involved in such rapid changes of depth. Acoustic efficiency must ultimately depend on the maintenance of fairly constant conditions of sound reflection and absorption round the essential organ of hearing.

The air sacs themselves are so extensive that their contraction would cause disruption of the adjacent musculature were it not for the intervention of some space-filling mechanism. It seems that the fibro-venous plexus which surrounds the sacs is ideally suited for this purpose, because there would be reciprocal filling of the plexus with reduction in the volume of the sinuses. A conventional venous plexus might be expected to be turgid at normal atmospheric pressure, but the pterygoid plexus of the cetacean is strongly adpressed between two sheaths of tough, fibrous tissue which, as previously stated, has been derived from the periosteum of the de-ossified pterygoid laminae. It is reasonable to suggest that the venous blood pressure, which is assumed to be zero at atmospheric pressure, must attain a value of at least two or three atmospheres before any swelling of the vessels could take place. There is also evidence to show that there is positive pressure in the pterygoid sinus under normal surface conditions if the squirting of foam from the newly cut sinus can be so interpreted. These factors suggest that the pterygoid cavities have an initial rigidity, and therefore a reserve capacity for withstanding hydrostatic pressure before appreciable diminution of the air cavity takes place.

If it is accepted that an air space is maintained in the middle ear cavity, it might be assumed that there would be a safe limit to the depth to which the cetacean can dive, after which fracture of the bulla would occur. The infrequency with which fractured bullae have been observed (Fraser & Purves 1953), suggests that there is a mechanism for overcoming this eventuality. As previously stated, Beauregard recognized the corpus cavernosus tympanicus as erectile tissue, but Bonninghaus and also the present authors have been unable to inject this body by manual pressure. It will be recalled that the lumen of the internal carotid in this body is extremely narrow and was thought by various anatomists to be degenerate. It is clear, however, that under the hydrostatic pressures available, the corpus could be erected by way of the internal carotid, in which eventuality it would occupy the tympanic cavity sufficiently to prevent fracture.

Unlike the lining of the air sacs, the tympanic cavity proper is lacking in the network of crypts and mucous ducts which are normally present in the lining of the air sacs, and mucous glands, if present at all, are poorly developed It seems highly probable that the foam in the sinuses is produced by secretions of the glands in association with the gaseous content of the air sinuses. In these circumstances, the air sinuses could be filled with foam leaving a foam-free cavity in the tympanic bulla. This foam-free cavity would diminish in volume with hydrostatic pressure and would, in extreme conditions, only occupy the vicinity of the auditory ossicles and fenestra rotunda. If the air sinus system reaches its limit of compressibility, there would be a pressure difference between the inside and the outside of the tympanic bulla because of the presence of the residual air cavities. It is suggested that this pressure difference is adjusted by the enlargement of the corpus cavernosum.

The question naturally arises as to how the contained nitrogen in the sinuses is prevented from passing directly into the blood stream in correlation with the increased pressure as the animal sounds. The first consideration is that this gas is not free to circulate in the air sinuses but is imprisoned in bubbles, the walls of which are composed of a mucus-oil dispersion. Bearing in mind the high solubility rate of nitrogen in fat, as compared with that in blood, and the very large total surface area of the oil constituent presented to the gas, (for instance 100 cc of oil reduced to particle size of 1μ would present a surface area of 1,200 sq.m.), it is reasonable to conclude that the nitrogen would be absorbed into the fat before becoming available for absorption into the blood. Conversely, with diminution of pressure, nitrogen would be liberated into the sinus system to augment the foam volume. This liberation of nitrogen would invariably be slower than the rate of decompression in a rapidly surfacing whale, so that there would be an accumulation of dissolved nitrogen in the foam. There is evidence that this nitrogen-charged foam is blown out at expiration (Fraser & Purves 1955).

It would seem that at all times during swimming and diving an equilibrium is maintained between (*a*) the hydrostatic pressure, (*b*) the rigidity of the tissues, (*c*) the turgor pressure of the blood vascular system, (*d*) the viscosity of the foam and (*e*) the volume of the gas as determined by the gas laws and by solution of the contained gas in the oil and mucus. The relative extent to which each factor operates to produce the equilibrium is beyond the scope of the present paper.

Acoustic Function of the Air Sacs

As previously stated, the air sinus system surrounds the periotic and occupies the space between that bone and adjacent cranial bones, and the periotic is itself separated osseously from the adjacent bones of the skull. With these factors operating it is necessary to discover the most effective sound path to the cochlea. The transmission or reflection of sound energy at the interface between two media depends upon the ratio of their acoustic resistances, and to some extent upon the frequency of the vibrations. Since the periotic is virtually surrounded by air space, the conditions are such that the interface can be regarded as being infinite in area as compared with the wave length, therefore the normal conditions of reflection of sound waves apply. According to Wood (1955) " Whenever the radiation resistances (of two media) are widely different there is almost complete reflection. The difficulty of transmitting sounds from water e.g. the noise of a ship's propeller in the sea, to the air-filled ear-cavity of an observer will be apparent." In fig. 30, from Wood, the graph shows the percentage energy of a sound wave reflected from a mass of bubbles in water. The percentage energy reflected is plotted as a function of the proportion of air to water. " This curve illustrates the serious reduction of intensity when a sound wave encounters a mass of air bubbles in the sea. The noise of a ship's propeller is seriously reduced by the bubbly water in the wake. In such cases the incident energy is partially reflected and partially absorbed, the loss increasing rapidly as the proportion of air to water increases." The graph refers to a layer of bubbly water of semi-infinite dimensions, but Rayleigh, according to Wood, has produced a formula for the reflection of plane waves from a layer of finite thickness :

$$\frac{\xi r}{\xi i} = r = \left(\frac{R_1}{R_2} - \frac{R_2}{R_1}\right) \Big/ \left\{4 \cot^2 \frac{2\pi l}{\lambda} + \left(\frac{R_1}{R_2} + \frac{R_2}{R_1}\right)^2\right\}^{\frac{1}{2}}$$

where r and i refer to the reflected and incident amplitudes, R_1 and R_2 ($= \rho_1 c_1$ and $\rho_2 c_2$) are the acoustic resistences of the medium (1) and the layer (2), l is the thickness, and λ the wave-length of the sound in the material of the layer. On the observed indication that the proportion of liquid to gas in the whale's ear foam is somewhere in the region of one to over a thousand, in the following calculation the proportion 1 to 10 can be accepted. As calculated from the following formula :

$$R_2 = \rho_2 c_2 = \sqrt{\frac{E_1 E_2 \{x\rho_1 + (1 - x)\rho_2\}}{xE_2 + (1 - x) E_1}}$$

where E_1 and E_2 refer to the elasticity of the two media $E_1 = 1{\cdot}2 \times 10^6$ and $E_2 = 2{\cdot}25 \times 10^{10}$; ρ_1 and ρ_2 the mean densities = 0·0012 for air and 1 for water and

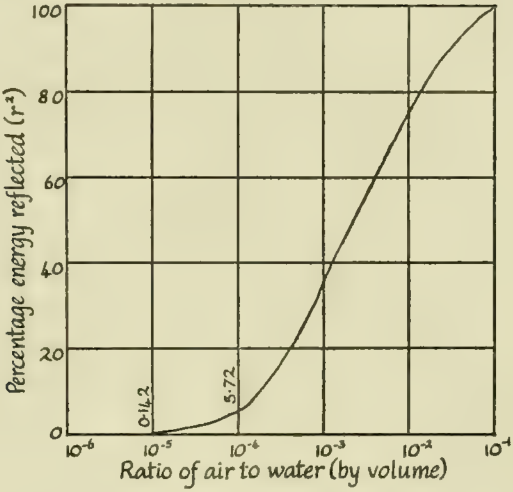

FIG. 30. Reflection of sound from air-water mixtures (after Wood, 1955).

x and $1-x$ refer to the proportions of the two constituents. The value for R_2 for a 1 in 10 mixture of water and air is then 348. If this figure is used in the first formula :

$R_1 = 1{\cdot}55 \times 10^5$ (for standard sea water)
$R_2 = 48$
$\lambda = 6{\cdot}8$ cm assuming a frequency of 50 kcs.
$l = 0{\cdot}5$ cm

the calculated result obtained is that 99·73% of the energy is reflected, that is assuming no loss through absorption. Since all sounds travelling in the direction of the cochlea by way of the bones of the skull and the soft tissues, with the exception of the meatus, must encounter the foam filled spaces, it is reasonable to assume that they must be almost completely reflected or absorbed.

Turning therefore to the meatus, in the Odontoceti it is open to the external surface of the tympanic ligament (which may be regarded as having the same acoustic resistance as the column of water filling the meatus) so that the first change of medium is that at the malleolar end of the ligament. The acoustic resistance of petrous bone must closely resemble that of ivory for which figures are available (Wood, 1955 p. 590). The velocity c_1 on a longitudinal bar is $2{\cdot}2 \times 10^5$ and the acoustic resistance $4{\cdot}1 \times 10^5$. The figure for the torsional velocity is not given but it may be assumed to be approximately a half the value for the longitudinal velocity. Employing the given figures for the acoustic resistance of water and ivory in the equation

$$r^2 = \left(\frac{\rho c_1 - \rho_2 c_2}{\rho c_1 + \rho_2 c_2}\right)^2$$

the result gives a figure of 45% reflection, but if the torsional velocity is used the figure will be 22% approximately. These figures refer to a bar of ivory of circular cross section, but the malleolar attachment to the tympanic ring is in the form of a channel girder with roughly half-tubular cross section, so that the rigidity coefficient, and hence the acoustic resistance, will be rather smaller than the figure quoted for ivory. Indeed it seems likely that the tympanic ligament transmits nearly all and reflects almost none of the incident energy. Assuming no slip at the incudo-malleolar joint, the molar vibrations of the malleus will be transmitted to the incus and thence to the stapes with very little loss of energy, since the incudal ligament is relatively minute in length and thickness. In the Mysticeti the inner part of the meatus is filled by the " ear plug " which consists of layers of cholesterol and keratinized epithelium (Purves 1955). It is an interesting fact that the acoustic resistance of paraffin wax is given as $1{\cdot}3 \times 10^5$ whereas that of sea water of 3·5% salinity is $1{\cdot}5 \times 10^5$ so that at the interface, the wax plug, if considered comparable, would form no appreciable barrier to sound waves.

It must be appreciated that the foregoing quantitative assessment is in the nature of an approximation, since all the formulae apply to simple, geometrical forms and not to a specialized, anatomical system adapted to a particular function. From these quantitative considerations, so far as sound reflection is concerned, there is no objection to accepting the meatus as the possible sound path.

Experimental Evidence of the Sound Conductivity of the Meatus

In order to test the relative suitability of the meatus from the absorption view point, a more precise experiment than that referred to in Fraser & Purves 1954, was carried out. A large portion of the squamo-mastoid region of a Fin Whale was obtained deep frozen and, when thawed, was dissected to expose the middle ear, the wax plug and meatus as far laterally as the blind portion. The blind portion was dissected to expose the cord connecting the inner part of the meatus with the external aperture. The output of a variable frequency oscillator was connected to a transducer by a concentric, screened cable. The transducer was in the form of a probe (see inset, Text-fig. 33), consisting of a steel cone cut transversely near its base for the insertion of a ceramic disc (barium titanate). A similar probe was connected to an amplifier and a cathode ray oscilloscope. The output of the oscillator was monitored by a rectifying voltmeter (see Text-fig. 32). A standard of reference was obtained by a calibrated deflection on the time base of the oscilloscope equivalent to 2 cm separation of the probes. The second probe was then moved in a mesial direction along the cord of the blind portion of the meatus and readings taken at 2 cm intervals (see Pl. 51). The readings consisted of increasing the volume of the oscillator until the deflection on the oscilloscope reached the reference level. Similar readings were taken for the inner portion of the meatus, the wax plug, the tympanic ligament, wax plug to ligament and fibrous tissue parallel with the meatus. The attenuation in decibels is plotted against the distance in centimetres in Text-fig. 31. The values shown are much greater than the known attenuation of sound in sea-water (16 dbs per thousand yards at 100 kcs) but the probes were set in the tissue and moved along an axis which was at right angles to direction of propagation of the sound waves so that the attenuation rate was grossly exaggerated. The attenuation would be still further exaggerated by the presence of any gas bubbles produced by decomposition prior to freezing but the latter, if present, were assumed to have been uniformly distributed in the tissues.

The graphs show a general, comparative picture of the attenuation in the various tissues involved at three different frequencies. The lowest attenuation rate at 100 kc was obtained in the blind section of the meatus immediately internal to the blubber. (The external, open portion of the meatus was not tested as it was considered that it would be filled with water under natural conditions.) The figure for 2 cm of the corium of the lumen of the meatus was slightly below the reference for 2 cm of the blind section but the attenuation rate of the whole length of the corium was slightly higher than for the blind section, and was comparable with the rate of attenuation of wax plug—wax plug— tympanic ligament. The curve for the fibrous tissue was based on readings taken 4 cm posterior to the lumen of the meatus. The initial power factor required for 2 cm of this tissue was 12 decibels above reference and the attenuation considerably higher than that for the lumen of the meatus. The attenuation for the corium through a distance of 8 cm to the end of the tympanic ligament was roughly comparable with the figure for an equivalent distance of the blind section. The attenuation of a transmission from the tympanic ligament to the thin end of the bulla, the distance being about 3 cm (i.e. 1 cm above the reference distance) was about 13·5 dbs, or equivalent to ca. 8 cm of the blind section. The attenuation between the corium of the meatus, adjacent to the wax plug and the end of the tympanic ligament, a distance of approximately 8 cm, was ca. 16 dbs.

From these qualitative results it would appear that any vibrations transmitted by the meatus, blind section, lumen or wax plug would be received at the malleolar end of the ligament at an intensity greater than that of vibrations from the same source transmitted simultaneously by the surrounding fibrous tissue. Underlying bone transmissions, conveyed through tissues further away from the meatus, would suffer reflection at the bulla-tympanic cavity interface. Since the sound transmitted by the meatal path would be dominant at any level of intensity, the animal must be subject to an intensity and/or phase difference at the two cochleae, due to the screening effect of the head and distance apart of the two meatal openings.

The graphs B and C show that the attenuation is rather lower at the lower fre-

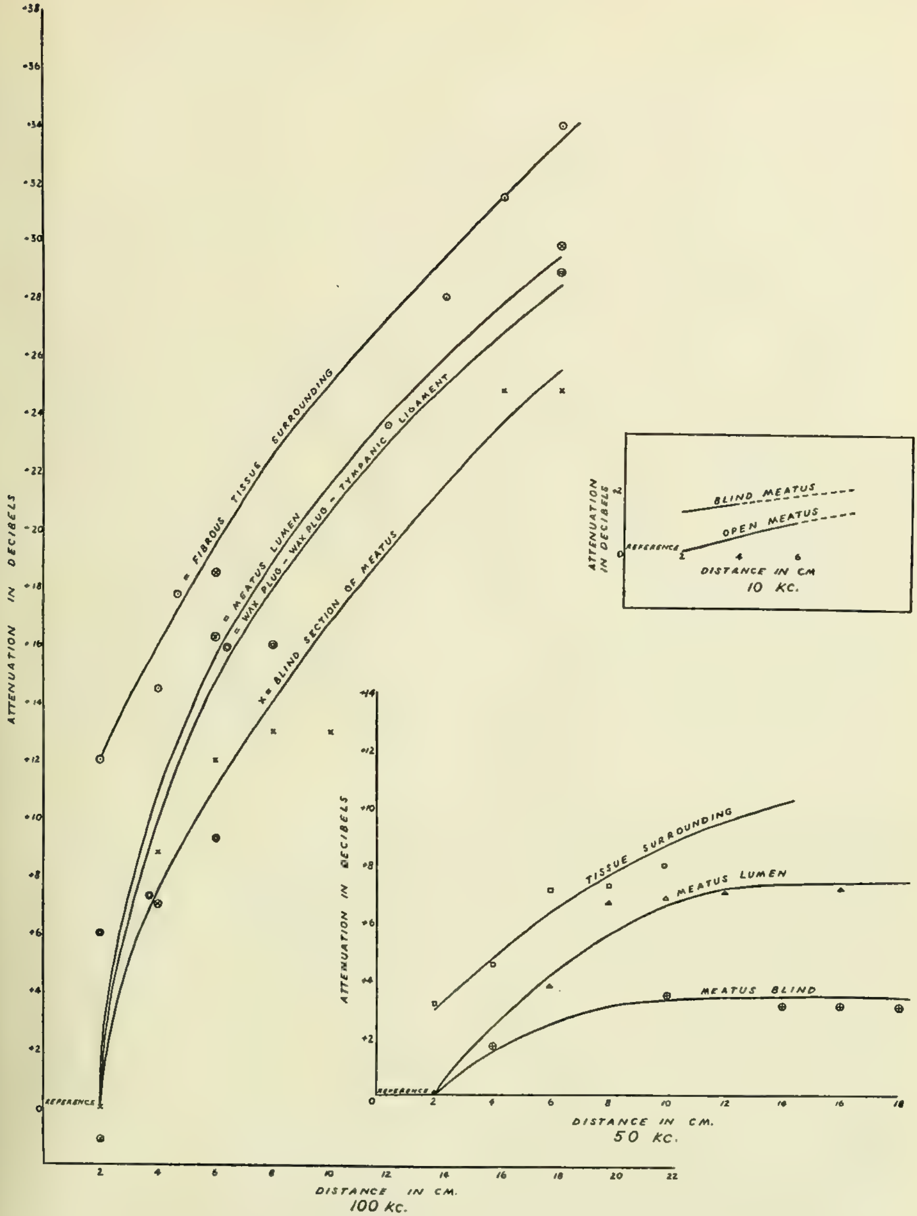

FIG. 31. Graph showing the attenuation of sound waves of 10–100 Kc in meatal and adjacent tissues of the ear of a Fin Whale.

quencies, a normal feature in sound vibrations. The reference level was adjusted to the reduced performance of the crystal at lower frequencies.

Similar tests to those just described were made on the external end of the external auditory meatus of a Sperm Whale. The results are compared with those obtained from the inner part of a Fin Whale meatus and are shown in Text-fig. 32.

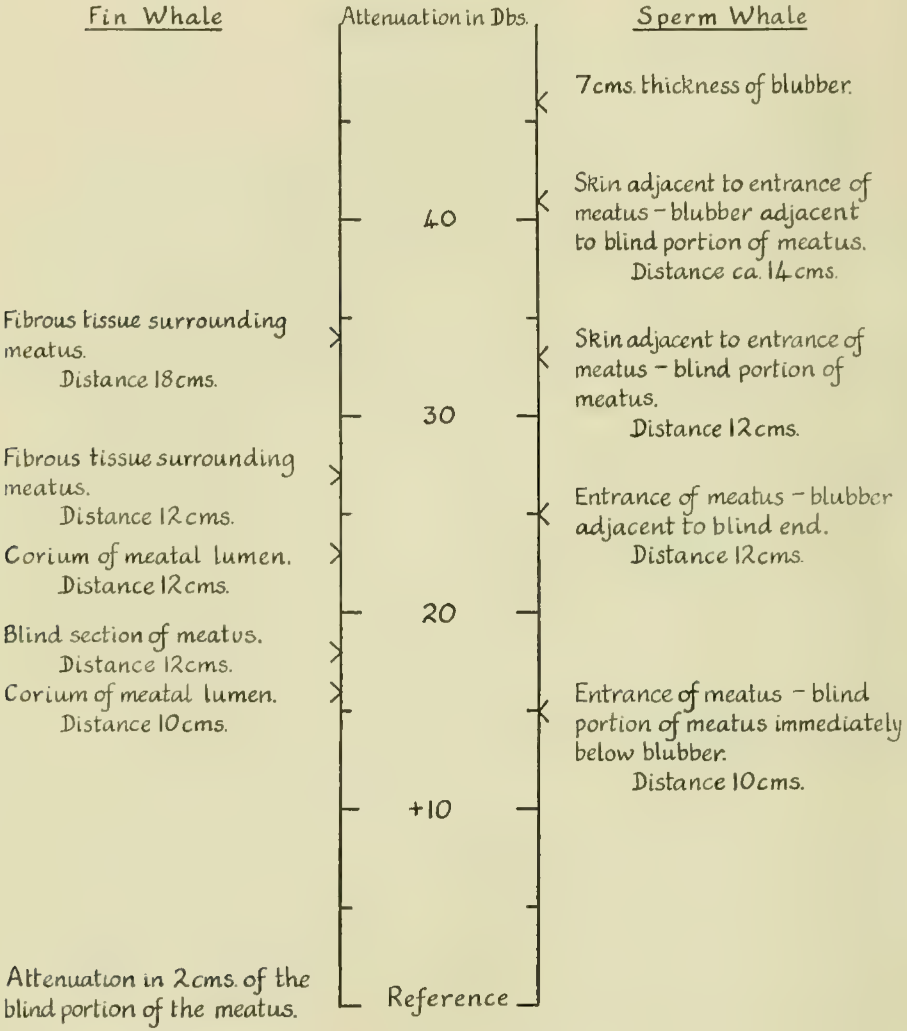

FIG. 32. Comparison of the sound conductivity of the external portions of the ear of a Sperm Whale with those of the inner portion of the meatus of a Fin Whale.

They indicate that the meatal lumen in both is similar in sound conductivity, and both are greatly superior to the adjacent blubber and fibrous tissue. It will be seen that 7 cm thickness of Sperm Whale blubber has a sound attenuation of 45 dbs above reference.

As previously described, the external surface of the tympanic bulla is encased in a closely adherent, fibro-elastic capsule some 10 cm. thick in a large whale. A slice of this tissue was tested for its sound conductivity. With 10 cm. of the tissue at 100 kc, the attenuation was approximately 8 dbs. above the reference, a figure some 5 dbs below that for 10 cm. of the blind section and approximately half that for 10 cm of the meatal lumen. This indicates that the acoustic impedance of the material of the capsule is high relative to that of the meatal tissue, and must have a highly damping effect on molar vibrations of the tympanic bulla, such vibrations being a characteristic of the function which some authors have assigned to this bone. It is submitted that one of the effects of the great weight and density of the tympano-periotic bones is the avoidance of forced oscillations of the bones within the frequency band of the animal's normal auditory range. It is clear, from the experiment described below, that the fused malleus is capable of undergoing high frequency oscillations up to 100 kc. It was found experimentally that these oscillations were transmitted to the thin involucral edge of the bulla, near the point of attachment of the malleus, but were subject to a power loss double that for an equivalent extent of meatal tissue. From this it would appear that vibrations transmitted from meatus to malleus would be greater in intensity than those transmitted from bulla to malleus. No signal could be obtained experimentally between malleus and periotic. It was proved experimentally that the malleus can undergo torsional vibrations independently of the bulla. Any molar, resonant vibrations of the latter would only vitiate the efficiency of the signal.

Experimental Evidence of Acoustic Matching

The question arises of the manner in which pressure amplitude is maintained and displacement amplitude increased. For the investigation of this problem, a thin steel wire was soldered to the end of one of the transducers, and the other end attached to the tip of the manubrium of the malleus at the normal point of attachment of the tympanic ligament, so that it simulated the latter in length and position (Text. fig. 33). The angle of attachment of the wire could be altered by raising or lowering the transducer, relative to the position of the manubrium, over a friction-free pulley, while the tension was kept constant by attaching a small weight to the cable connecting oscillator and transducer. The incus was allowed to rest on the malleus in its natural position, separated from the latter by a thin film of petroleum jelly. The stapes was simulated by the stylus of a micro-groove, crystal pick-up, which was connected to an amplifier and oscilloscope. The frequencies used in this experiment lay between 10 and 100 kc. A considerable difference was noted in the height of the deflection of the time base in relation to the angle which the wire made with the long axis of the manubrium mallei. When the wire was pulling at a sharp angle, approximately 5°, the deflection was about ten times the height attained when the wire was pulling at right angles to the manubrial axis. The only acceptable interpretation of this evidence is that the malleus was being thrown into torsional vibrations, and that the manubrium was behaving like a crank, actuated by the piston-like movements of the crystal face. When the wire was pulling at right angles to the manubrium, the relationship between the pressure-displacement amplitudes of the crystal face and the manubrium would be approximately unity; whereas, when the wire was pulling at a sharp angle to the manubrium, the displacement ratio would be increased. Thus in the middle ear of the cetacean there exists a mechanism for the increase of displacement amplitude of water-borne sounds. It might be pointed out that this method of amplification is self-compensating, since the smaller the displacement amplitude of the sound wave the greater the relative amplification.

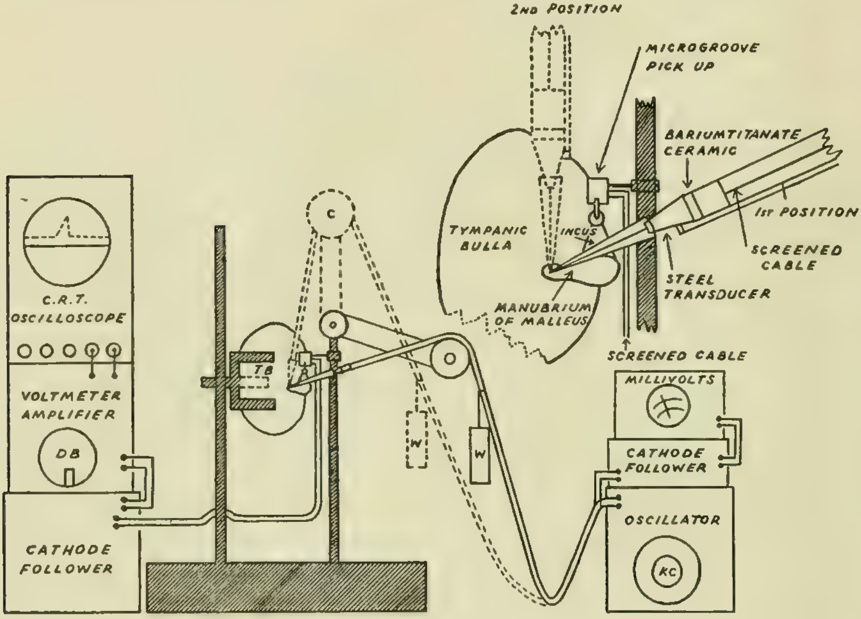
2ND POSITION
MICROGROOVE PICK UP
BARIUMTITANATE CERAMIC
1ST POSITION
SCREENED CABLE
STEEL TRANSDUCER
TYMPANIC BULLA
INCUS
MANUBRIUM OF MALLEUS
SCREENED CABLE
C
C.R.T. OSCILLOSCOPE
VOLTMETER AMPLIFIER
DB
CATHODE FOLLOWER
TB
W
W
MILLIVOLTS
CATHODE FOLLOWER
OSCILLATOR
KC

FIG. 33. Diagram of apparatus for demonstrating changes in the amplitude of torsional oscillations of the malleus when actuated by a simulated tympanic ligament vibrating longitudinally at various frequencies and angles of traction.

Text-fig. 34*a* shows the relationships of the tympanic membrane and auditory ossicles in a terrestrial animal such as man. Assuming the ratio of manubrium of the malleus to the long process of the incus as 2 : 1, then the displacement amplitude ratio between the tympanic membrane and the stapes is also 2 : 1. Text-fig. 34*b* shows the arrangement in the cetacean. The manubrium is shortened, so that its length is approximately that of the long process of the incus; the tympanic membrane is closed up into a flat ligament which pulls at a sharp angle to the axis of the manubrium. In this case there is an amplification factor dependent upon the length of the manubrium and the angle of attachment of the ligament (Text-fig. 34*c*). Assuming this amplification factor to be 30 : 1, then the displacement amplitude at the stapes of a sound wave in water (of which the displacement amplitude for the same intensity and frequency is 1/60 that of the same sound air-borne) would be equal to that experienced by the terrestrial mammal.

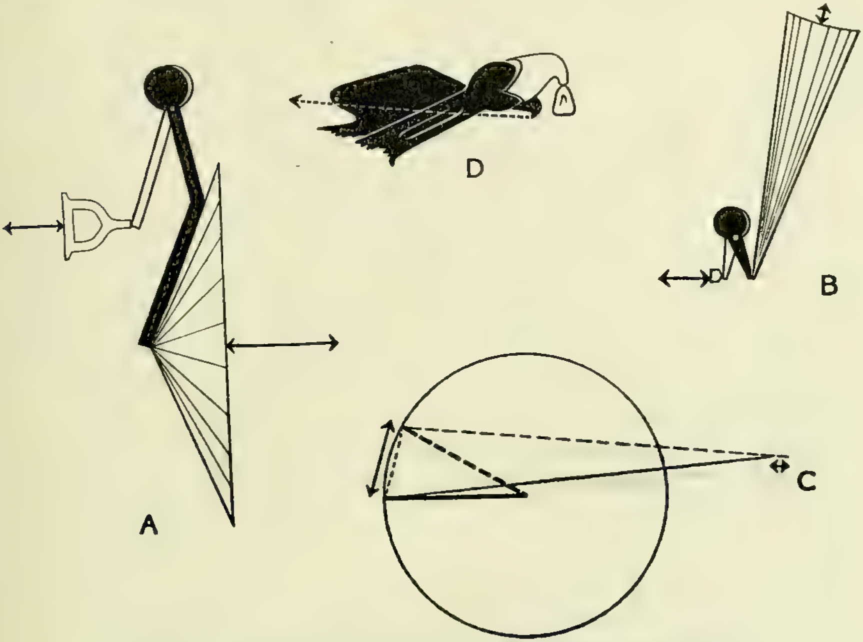

FIG. 34. Schematic representation of the ossicular mechanism.

a. Terrestrial mammal in antero-posterior view.

b. Cetacean ,, ,, ,, ,,

c. The mode of amplification of lateral displacement of the tympanic ligament by means of a crank system.

d. The buttressing function of the sigmoid process against lateral movement of the malleus, and the articulation of the latter with the incus.

In man, the pressure at the oval window of the inner ear is determined by the ratio between the area of the ear drum and that of the foot of the stirrup bone, as well as by the leverage of the auditory ossicles. The ratio is 30 : 1, the leverage approximately 2 : 1 giving a pressure ratio between the stapes and drum of about 60 : 1, which is approximately the same pressure amplitude ratio between a sound wave of the same intensity and frequency in water and air.

In order that the pressure amplitude at the cochlea in the cetacean be the same as that in terrestrial mammals, some compensation has to be made for the reduction in pressure due (*a*), to the 30 : 1 displacement amplification factor described above, and (*b*), to the reduction in area of the tympanic membrane resulting from its modification from the membranous, drum-like structure of terrestrial mammals into the ligament of the cetacean. It is submitted that the compensation is achieved by the reduction in the cross-sectional area of the stapes, so that the ligament-stapedial area relationship remains approximately 30 : 1 as in terrestrial mammals. Inspection of dissected specimens indicates that the ratio in the cetacean is of that order (see Pls. 49, 50 and 53).

For the same intensity and frequency, the pressure amplitude of water-borne sounds is 60 times greater than in air. Accepting the ligament-stapedial area ratio as 30 : 1, and the reduction in pressure due to the leverage at the manubrium as 1 : 30, then the pressure of a water-borne sound at the cochlea is also 60 times greater than a sound of the same intensity and frequency in air. This is the calculated pressure increase experienced in man. In the experiment described on p. 128 the minimum angle of attachment of the wire to the manubrium mallei was about 5°. In order to obtain the amplification factor required in the cetacean ear the angle would require to be approximately 2°. It can be seen from Pls. 49, 50 and 53 that the angle is of that order.

Since the pressure amplitude of sound presented at the fenestra ovalis of terrestrial animals is the same as that received at the inner ear of aquatic lower vertebrates, the evolution of the cochlea would seem to be linked with the increased displacement amplitude of air-borne sounds.

Discrimination and Directionality

Text-fig. 34*d* shows schematically the attachment of the processus gracilis of the malleus to the sigmoid process of the bulla and the articulation of the malleus with the incus. It will be noted that the processus gracilis is of a channel-girder construction ; its attachment to the sigmoid process is of extremely thin bone. The arrow indicates the direction of the long axis of the tympanic ligament. Traction or pressure along the line of this axis would result in rotation of the head of the malleus about the long axis of the processus gracilis, since lateral movement is prevented by the buttressing effect of the sigmoid process. The rotation imparts a 'screw-driver' movement to the incus which in turn rotates about its forwardly projecting, short process (not shown in figure). That is to say, it is exactly the same as in terrestrial mammals. If, in spite of the buttressing effect of the sigmoid process, the malleus were to undergo lateral movement, the articular facets of malleus and incus would simply slide over one another without imparting any movement to the incus. If oscillatory movements in either of the directions at right angles to the axis of the ligament are assumed, then positive movement of the incus is possible in the first phase of the first oscillation only. In the second phase the bones would be partially disarticulated, so that the movement of the malleus would be expended in taking up the gap between the facets. It will be recalled that the short process of the incus is attached by a ligament to the periotic, so that vibrations of the bulla (to which the malleus is attached), resulting in movements of the malleus in any of the directions other than the rotational one, would not be transmitted to the incus. This has been proved experimentally by subjecting a large working model of the auditory ossicles and their attachments to the types of vibration described above. The unique effectiveness of the rotational movement of the malleus is one of the fundamental reasons why theories involving vibrations of the tympanic bulla (e.g. the resonance theories of Lillie & Kellogg and the seismic theory of Yamada) are not accepted by the present writers, who believe that the comparable articulation in man and other mammals serves the same function of preventing resonant vibrations of the bulla and/or adjacent bones from reaching the cochlea. Transmission to the cochlea of vibrations of the bones of the skull or the bulla, and of all parts with the exception of the tympanic membrane, would be accompanied by loss of directionality of hearing.

The conditions of sound transmission in water are such that cetaceans must normally be subjected to noise intensity levels quite outside the experience of terrestrial mammals, and yet the construction of the cochlea is such that the ear must be sensitive to the same threshold levels as those experienced by land mammals. For example, Fletcher & Wegel according to Wood (1955) have found that at a frequency of 2000–2500 p.p.s. the human ear can respond to a pressure amplitude of the order of 10^{-3} dyne/cm^2 or 10^{-9} of an atmosphere. He states that in air this corresponds to a displacement amplitude of 10^{-9} cm which is about 1/30 of the diameter of a molecule of oxygen, or 10^{-4} of the mean free path of the molecules in air at N.T.P.

In view of the high noise intensity in water and the great sensitivity of the cochlea, it is not surprising that the cetacean meatus is of very small calibre. It is almost certain that a mechanism exists to protect cetaceans against the harm that excessive noise can cause.

Most mammals are provided with muscles for closing the meatus, and even in man the vestiges of these remain and may be stimulated by electrical current (Beattie 1932). In the Cetacea, although the pinna has disappeared, its cartilages and muscles are to a greater or lesser degree present beneath the blubber. The m. occipito-auricularis profundus and the m. zygomatico-auricularis described and figured by Boenninghaus in *Phocaena* (Pl. 1, D) seem suitably placed to control the tension and aperture of the external meatus in the Odontoceti. In the Mysticeti, Denker (1902) described a number of muscles attached to the blind portion of the meatus which presumably have the function of increasing or relaxing the tension of this part of the tube (see also p. 135).

It is concluded that the meatus is the most favourable sound path as in terrestrial mammals, and, as in the latter, the same conditions for directional hearing obtain, which are—the degree of separation of the ears, the screening effect of the head and the association that these have with phase and intensity differences. In terrestrial mammals such phase and intensity differences can quickly be assessed by the animal, even when in motion, by adjustments in the orientation of the ears and head. The Cetacea, lacking external ear pinnae and the degree of freedom of orientation of the head which a well-defined neck gives, might be expected to have some kind of compensating facility. Essentially, directionality is obtained by equating the sound intensity at the two cochleae. It was found experimentally that the sound conductivity of the cetacean meatus could be increased or decreased by varying its tension. It is suggested that this equation of pressure at the cochlea is achieved by the traction of the auricular muscles on the meatal tube. The great development of the pterygoid muscles, despite the reduced lateral mobility of the lower jaw, and the mode of attachment of these and the tensor palati muscles into the walls of the air sacs, seem to suggest that they have a second function related to the air sac system. As already suggested (Fraser & Purves, 1953), the arrangements which exist in terrestrial mammals for making small, temporary adjustments to the tension of the tympanic membrane are also present in the Cetacea but, due to the large adjustments required for the rapid changes of pressure with changes of depth, it is doubtful if the tensor tympani muscle is as effective in this respect as it is in terrestrial mammals. It is suggested that this function might well be performed by the palatal and pterygoid muscles. It is interesting to note that when humans are subjected to abnormal pressures, whether in diving or in aircraft, adjustment of the pressure in the middle ear is obtained by swallowing, in which both pterygoid and palatal muscles are brought into operation. The general arrangement of the air sac system could also be of value in direction finding.

THEORIES OF CETACEAN HEARING

Dr. Yamada's contribution to the *Anatomy of the Organ of Hearing in Whales* (1953) was received while the present paper was in preparation. Among other conclusions reached by him are that the external meatus is vestigeal, that the auditory bones are not acoustically isolated, and that the tympano-periotic bone is " a dynamic unit of seismographic principle ".

Yamada's conclusion that the external meatus is vestigeal is based on the unjustifiable assumption that it is unable to transmit sound vibrations. He assumes that the sound waves to be transmitted have the same physical properties as those received by terrestrial mammals. In all specimens examined by him he has found a continuous cord of tissue from the external to the internal portion of the meatus, and it has been proved experimentally by the present writers that this path is an efficient conductor of longitudinal vibrations. This was also proved for the tympanic ligament, contrary to Yamada's conclusions (p. 46). In order to justify the refutation of the acoustic isolation theory he cites the case of *Platanista* in which, according to Hyrtl, the tympano-periotic is fused to adjacent skull bones. As previously pointed out (p. 43) all the specimens of *Platanista gangetica* available for examination in connection with the present paper had tympano-periotic bones which were not thus fused, in this agreeing with other cetaceans. Yamada also points to the strong, fibrous connection of the periotic in *Balaenoptera physalus* which passes through a canal bordered by the pterygoid and squamosal bones. The feature referred to in his fig. 18, p. 44 is the foramen ovale and the course he describes for the ligament to lower jaw is that followed by the mandibular branch of the 5th nerve. He states that the fibrous connections negative the idea of acoustic isolation, but it may be pointed out that the only fibrous connections are those derived from the periosteum of resorbed bones of the tympano-periotic hiatus. This periosteum sheathes the periotic and thus is very unfavourably situated for the transmission of vibrations to the petrous bone. The acoustic resistance of the two substances are such that on theoretical grounds about 50% of the incident energy would be reflected, assuming the most favourable conditions of vibrations normal to the surface of the bone.

With regard to Boenninghaus' Schalltrichter theory, it has already been stated by Fraser & Purves (1955) that sound waves could not be transmitted to the funnel of the bulla by way of the air in the pterygoid sinuses because of the presence of the albuminous foam in the sinuses. Considering the possibility of transmission of vibrations from the lateral wall of the sinuses through the mucous membrane of the tympanic funnel to the tympanic ligament, sound waves emanating from a source lateral to the body of the animal would have to pass through the thickness of blubber, muscles, mandible, intra-mandibular fatty tissue, vascular networks and subsequently be transmitted in a direction at right angles to that of the original direction. This would involve shearing stresses on the mucous membrane which are much more easily damped out than longitudinal ones. When there exists a simple, direct sound path, from the external meatus to the tympanic membrane, of a homogeneous histological structure, and of which the ligament is a prolongation, it is difficult to accept an explanation which involves an extremely tortuous path with powerful acoustical barriers.

The adaptation of the sound path normal to terrestrial mammals is, on the face of it, more acceptable than any *de novo* method of sound conduction in mammals.

With reference to Yamada's criticism of Boenninghaus' Schalltrichter Theory, while not accepting the latter, it is possible to reply to Yamada's unanswered question "How can the vibration of the malleus alone be undamped in spite of its rigid connection with the bulla?" The functioning of the malleus is stated in Fraser & Purves (1954) p. 110, where it is also shown that vibrations of the bulla cannot be transmitted beyond the malleus.

Yamada summarizes his seismographic explanation by stating that the heavy involucrum (of the tympanic bulla) is the weight of a pendulum, in relation to which the malleus is motionless, so that vibrations of the involcrum are conveyed to the essential organ of hearing. Essentially this idea differs little from that of Kellogg (1938) or from the original explanation of Lillie (1915). The objections to it are that (*a*) if the bulla did act like a pendulum and undergo total vibrations, the axis of rotation would be through the two thin, supporting pedicles mentioned by Kellogg. It has been shown (Fraser & Purves, 1953) that the articulation between the malleus and incus is specifically arranged to avoid such vibrations, being transmitted beyond the junction of the malleus and incus; (*b*) it is well known that all pendulums oscillate at a fixed frequency depending on the length of the lever. It is difficult to understand how a heavy pendulum of the magnitude of the bulla could (with the limit of power available in a sound transmitted in water) be forced to vibrate at a frequency of 100,000 cycles per second a frequency to which at least one kind of cetacean (Schevill & Lawrence, 1953) is known to be sensitive.

In another paper (Schevill & Lawrence, 1953), received while the present work was in preparation, it was noted that in the authors' hearing experiments on *Tursiops truncatus* there was a marked drop in positive response at 120 kc and final lack of response to frequencies above 130 kc per sec. These authors assumed that the mode of hearing in their experimental animal was by bone conduction, yet they themselves mentioned the fact that there is no evidence of an upper frequency limit to bone conducted sound in man ; the highest pitch that is normally audible continues to be heard even when the subject is exposed to much higher frequencies. They quote Kunze & Kietz (1849) as having published curves reaching 128 kc for man without any sign of a break in the upper end of the curve. They consider, in the light of the bone conduction evidence when man is the subject, that there should be no upper limit to hearing in cetaceans, but their experimental findings provide sufficient evidence to suggest that bone conduction is not involved. It has previously been pointed out that it would be very undesirable to have this mode of hearing from the point of view of its lack of directionality.

In a recently published, very comprehensive work on hearing in whales, Reysenbach de Haan (1957) has shown by experimental and quantitative treatment of the anatomical data that the conclusions reached by the writers (Fraser & Purves, 1955) are in almost every respect in agreement with his own. He does not however concur with the hypothesis that the sound is conducted to the middle ear by the external auditory meatus. His work was received some time after the completion of this paper, and because of the disagreement referred to above it will be necessary to supplement the observations on the external meatus already referred to (pp. 108–112 *supra*) by additional evidence obtained from a gross dissection of the ear of a Fin Whale.

Before proceeding with this account, it is necessary to refer to a disparity between the present writers' and Reysenbach de Haan's interpretation of the Schalltrichter Theorie of Boenninghaus. It is evident from Reysenbach de Haan's conclusions that he regards "schalltrichter" as being synonymous with "tympanic annulus" but this is not so. Quoting from Boenninghaus "the whole processus anterioris of the tympano-periotic is in the shape of a funnel the anterior diameter of which is about 1 cm . . . also quite remarkable is the anteriorly concave hearing wall and the sigmoid process which bounds the funnel from behind". It will be seen from this that the entrance to the funnel or "shell" as he subsequently calls it lies at the anterior end and not lateral to the tympanic bulla.

In addition, the tympanic annulus of *Delphinus* is never as large as 1 cm in diameter and the sigmoid process lies anterior to, and is not "behind", the annulus. Boenninghaus goes on "the funnel has through the aforesaid turning of the tympanic bulla been turned forward so that sound waves from the rear do not strike it. . . . The bony sound funnel is now to be regarded as the functioning substitute of the pinna and auricular passage of land mammals". Boenninghaus' sound path is stated as follows—"Sound waves from the side and front pass through skin, fat, tongue and jaw bone musculature—through the anterior opening of the bulla to the anterior process of the malleus thence through the immovable incus and stapes to the fenestra ovalis."

Pl. 51 shows a dissection of the auditory apparatus of a 60-ft Fin Whale caught near Steinshamn, Norway, 1956. It will be noticed that the whole external meatus is stretched tightly and lies on an approximately straight, horizontal axis from the middle ear to the external aperture. The feature is not an artifact of preservation but was found to be the condition in all the freshly killed whales examined at Steinshamn. The attenuated, distal, closed end of the meatus passes through a conspicuous auricular cartilage to which are attached five robust, auricular muscles none of which is less than 5 cm in diameter. Dorsal to these muscles is an extensive retial mass of blood vessels which probably indicates that the muscles are functional. The proximal portion of the meatus, the corium of which contains the ear-plug, lies in a deep groove between the exoccipital and squamosal bones and in life was surrounded by loose connective tissue and oil sinuses. Enveloping the whole of this area, and adhering to the bones, there was in life, a great mass of dense, white, fibrous tissue about 30 cm in thickness and with tough unyielding fibres forming a close reticulum throughout the entire mass. The meatus was thus enclosed in a tunnel formed dorsally by bone and ventrally by the white fibrous tissue. In these circumstances any contraction of the auricular muscles would result in considerable stretching of the meatal wall and of its closed, distal extremity.

Turning now to the proximal end of the meatus, the same dissection, Pl. 52, shows that the ear-plug, which fills the lumen of the meatus, is closely applied to the external surface of the " glove finger ". In the dissection the plug has been bisected to show the " annual rings " but in life it would completely envelop the " glove-finger ". Owing to decomposition, the ear-plug has become detached from the stratum germinativum, but in life it forms the zona cornea of the " glove-finger " and meatal epidermis and is consequently very firmly attached to the latter structures. Pl. 53 shows the middle ear after removal of part of the bulla and periotic. Originating on the mesial aspect of the internal face of the bulla anterior to the tympanic annulus, there is a short, stout muscle the insertion of which merges into the fibrous matrix of the internal wall of the glove finger opposite the tympanic ligament. Contraction of this muscle would result in movement of the whole of the " glove-finger ", and of the ear-plug assembly, as far as the lateral, blind end of the meatus. In this respect the auricular muscles and the small muscle referred to above would act antagonistically. Mobility of the external meatus implied in the anatomical arrangement would be superfluous if the meatus were non-functional.

In terrestrial mammals the special senses, of hearing, scent and sight are all available for the perception of the animal's environment. In the Toothed Whales the olfactory sense is wanting, and in the Baleen Whales, if present at all, it is very greatly reduced. However efficient the eyes may be, their function must be limited by conditions of turbidity of the water and by depth. Some River Dolphins may be totally blind. In all cetaceans the sense of hearing is the most important of the special senses.

CONCLUSIONS

It is concluded from the examination of specimens, from the evidence of existing literature and from the results of experiments that:

(1) the configuration of the ventral aspect of the cetacean skull, which is associated

with the development of air spaces, provides a fairly reliable guide to the systematic arrangement of the Order Cetacea.

(2) The Mysticeti as a whole are more primitive than the Odontoceti.

(3) In the Odontoceti there is a gradation of development and specialization of the sinus system within the sub-order as a whole, from the relatively primitive River Dolphins through the estuarine forms to those which are pelagic. There are distinct series of gradations within the sub-divisions of the hierarchy, intra-generic as in the species of *Lagenorhynchus* ; within the sub-family, as in the genera included in the Delphininae ; within the family, as in sub-families included in the Delphinidae ; and within the super-family, as in the families represented in the Delphinoidea.

(4) The systematic arrangement of the order in the present paper fits basically into the framework of Simpson's (1945) classification, but has been extended in detail.

(5) A notable exception is in the elevation of the Monodontinae to super-family rank.

(6) The elaborate sinus system of the Cetacea consists almost entirely of an extension of the middle ear cavity into the lamina of the pterygoid bone involving invagination, distension and extension of the latter.

(7) The peribullary sinus is derived from the invasion of the basioccipital crest and squamosal bone by the tympanic cavity after dissociation of the tympano-periotic from the adjacent cranial bones.

(8) Hearing is by way of the external auditory meatus as in terrestrial mammals.

(9) Hearing is precisely discriminative and directional, and the ear is sensitive to a wide range of frequencies.

(10) The qualities of hearing referred to have been achieved by modification of typically mammalian auditory structures ; so far from being non-functional, the meatus, the tympanic membrane, the auditory ossicles, tympanic bulla, the cochlea, the tympanic cavity and sinus system are all perfectly adapted for underwater hearing.

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KEY

A —Artery.
AAS —Accessory air sinus.
AC —Auricular cartilage.
ACE —External carotid artery.
ACI —Internal carotid artery.
AL —Lachrymal artery.
ALS —Alisphenoid bone.
ALS(LL)—Lateral lamina of alisphenoid.
ALT —Anterior ligament.
AM —Mandibular artery.
AMI —Internal maxillary artery.
AO —Orbital artery.
AOF —Antorbital foramen.
AP —Anterior pedicle.
APPB —Palato-pharyngeal branch of internal maxillary artery.
APT —Pterygoid artery.
APTMB —Arterial branches to internal pterygoid muscle.
AS —Anterior sinus.
AT —Temporal artery (deep).

B —Bone.
BC —Calcified element of bone.
BL —Blubber.
BO —Basioccipital bone
BOC —Basioccipital crest.
BR —Resorbed element of bone.
BS —Basisphenoid bone.

C —Cochlea.
CAP —Capillary.
CC —Corpus cavernosum.
CF —Fat cells.
CRH —Cranial hiatus.

DMU —Mucous duct.

EAM —External auditory meatus.
ECI —Ciliated epithelium.
ECO —Columnar epithelium.
EP —Ear-plug.
ET —Eustachian tube.
EXO —Exoccipital bone.

FEO —Fenestra ovalis.
FER —Fenestra rotunda.
FG —Fat globules.
FO —Foramen ovale.
FOI —Infundibulum of foramen ovale.
FP —Falciform process.
FR —Frontal bone.
FR(OR) —Orbital process of frontal bone.
FR(PO) —Post-orbital process of frontal bone.
FR(PR) —Pre-orbital process of frontal bone.
FT —Fatty tissue.
FVP —Fibro-venous plexus.

GL —Glove-finger.
GMU —Mucous gland.
GOC —Goblet cell.

I —Incus.
ILS —Interlaminar space.
IMFB —Intra-mandibular fatty body.

JU —Jugal bone.

LA —Lachrymal bone.
LI —Ligamentum incudis.
LS —Lymph space.

M —Muscle.
MA —Malleus.
MAS —Mastoid process.
MD —Mandible.
MEP —External pterygoid muscle.
MFS —Striped muscle fibres.
MIP —Internal pterygoid muscle.
MLO —Longitudinalis oesophagi muscle.
MLP —Levator palati muscle.
MM —Masseter muscle.
MO —Orbital muscle.
MOO —Orbicularis-oris muscle.
MPP —Palato-pharyngeus muscle.
MPP(E) —Palato-pharyngeus muscle (pars externa).
MPP(I) —Palato-pharyngeus muscle (pars interna).
MPP(S) —Palato-pharyngeus sphincter.
MS —Middle sinus.
MSC —Superior constrictor muscle.
MSP —Salpingo-pharyngeus muscle.
MT —Temporal muscle.
MTHP —Thyro-palatinus muscle.
MTP —Tensor palati muscle.
MUM —Mucous membrane.
MX —Maxilla.
MAX —Maxilla (figs. 15–21).
MXC —Maxillary crest.
NA —Auditory nerve.

NM —Mandibular branch of trigeminal nerve.
NO —Optic nerve.
OC —Occipital condyle.
OF —Optic foramen.
OI —Optic infundibulum.
OS —Orbitosphenoid bone.

P —Periosteum.
PA —Palatine aponeurosis.
PAL —Palatine bone.
PAL(LL)—Lateral lamina of palatine bone.
PAO —Paroccipital process.
PAR —Parietal bone.
PBS —Peribullary sinus.
PE —Periotic.
PG —Processus gracilis.
POS —Posterior sinus.
PP —Posterior pedicle.
PRS —Presphenoid bone.
PS —Periosteal sheet.
PT —Pterygoid bone.
PTF —Pterygoid fossa.
PTH —Pterygoid hamulus.
PT(IL) —Inferior lamina of pterygoid bone.
PT(LL) —Lateral lamina of pterygoid bone.
PT(ML) —Mesial lamina of pterygoid bone.
PTS —Pterygoid sinus.
PTS(PO)—Post-orbital lobe of pterygoid sinus.
PTS(PR)—Pre-orbital lobe of pterygoid sinus.
PI(SL) —Superior lamina of pterygoid bone.

S —Air sinus.

SB —Secondary bone.
SC —Semicircular canal.
SM —Stapedial muscle.
SO —Supraoccipital bone.
SP —Sigmoid process.
SQ —Squamosal bone.
SQZ —Zygomatic process of squamosal.
ST —Stapes.

TA —Tympanic annulus.
TB —Tympanic bulla.
TB(PA) —Posterior aperture of tympanic bulla.
TC —Tympanic cavity.
TF —Fibrous tissue.
TL —Tympanic ligament.
TM —Tympanic membrane.
TP —Tympano-periotic bones.
TSQR —Tympano-squamosal recess.
TT —Tensor tympani muscle.

V —Vomer.
VIJ —Internal jugular vein.
VIM —Internal maxillary vein.
VM —Mandibular vein.
VN —Vein.
VP —Venous plexus.
VPT —Pterygoid vein.
VTEP —Ventral tendon of external pterygoid muscle.

ZA —Zygomatic arch.

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PRESENTED

EXPLANATION OF PLATES

PLATE I

Phocaena phocoena (from Boenninghaus, 1903, his Plate 12, figs. 3, 4, 5 and 2).

(A) Ventral view of the soft parts of the pterygoid region.
(B) Ventral view of the right side of the pterygoid region 1 cm deep to figure A.
(C) Same view 1 cm deep to figure B.
(D) View of the right side of head after removal of subcutaneous muscle and fat.

The numerals used in the figures are referred to in the text.

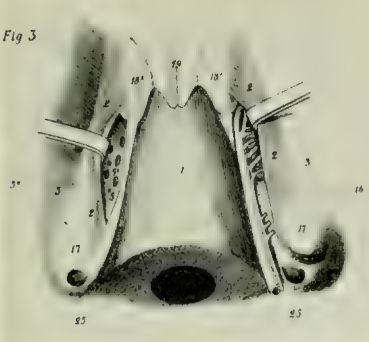


Fig 3
19
18'
18'
2
2
2
2
3
3
3'
1
2
16
17
17
25
25

A

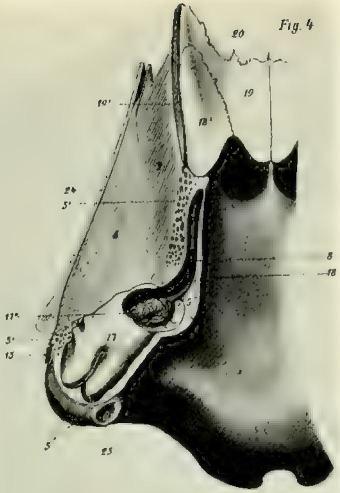


Fig. 4
20
19'
19
18'
24
5'
6
8
18
17
5'
13
5
25

B

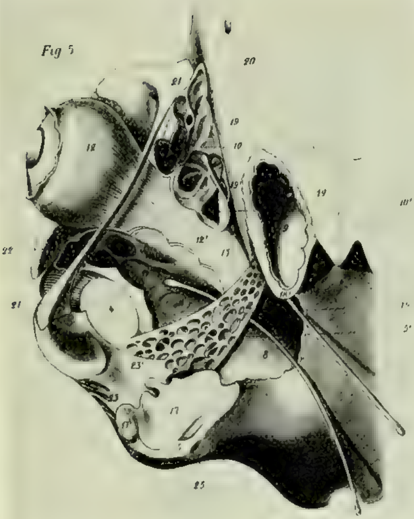
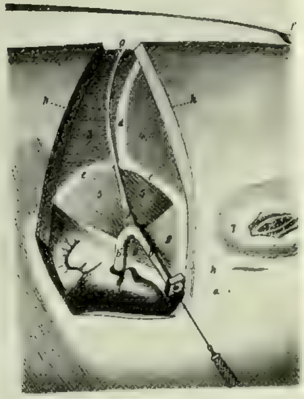


Fig 5
20
21
19
10
18
19
10'
22
12'
13
21
8
23'
23
17
25

C


f
g
h
k
d
d
e
5
5
7
8
b
h
a

D

PLATE 2

Sections of the mucous membrane of the pterygoid sinus of *Globicephala melaena*.

(A) Section cut in a plane parallel with and near to the surface of the mucous membrane (× 50).

(B) Longitudinal section of the pterygoid sinus lateral wall (× 160).

(C) Enlarged portion of mucous gland shown in figure B (× 600).

PLATE 2

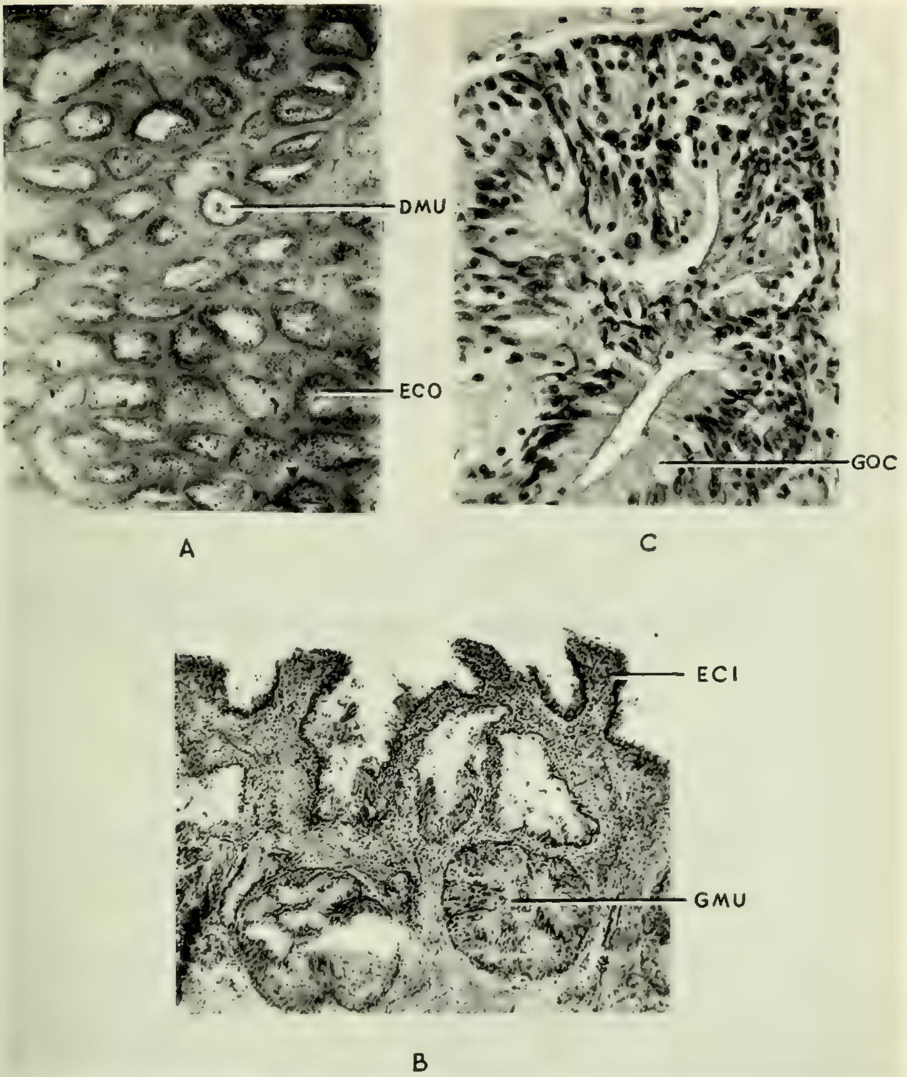
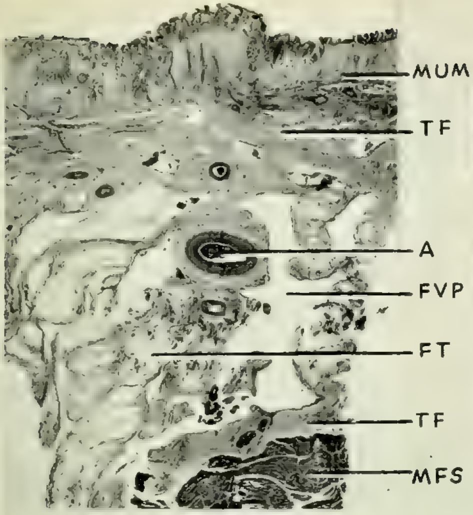
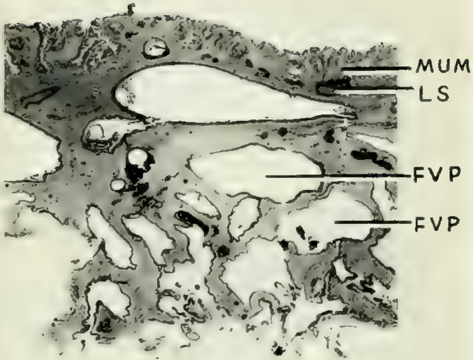

DMU
ECO
A
GOC
C
ECI
GMU
B

PLATE 3

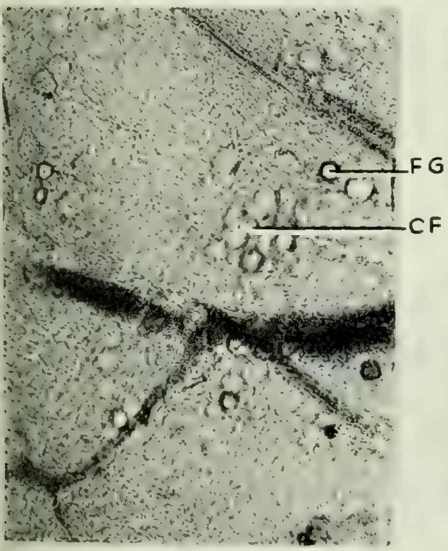
(A) Longitudinal section through the lateral wall of the pterygoid sinus (× 8).
(B) Longitudinal section through the mesial wall of the pterygoid sinus (× 8).
(C) Section cut in a plane parallel with [and deep to that shown in] Plate 2, figure A (× 100).
(D) Section showing contents of lymph spaces (LS) (× 1000).


MUM
TF
A
FVP
FT
TF
MFS

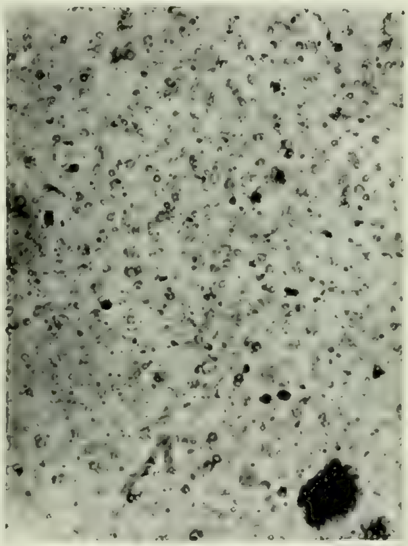
A


MUM
LS
FVP
FVP

B



C



D

PLATE 4

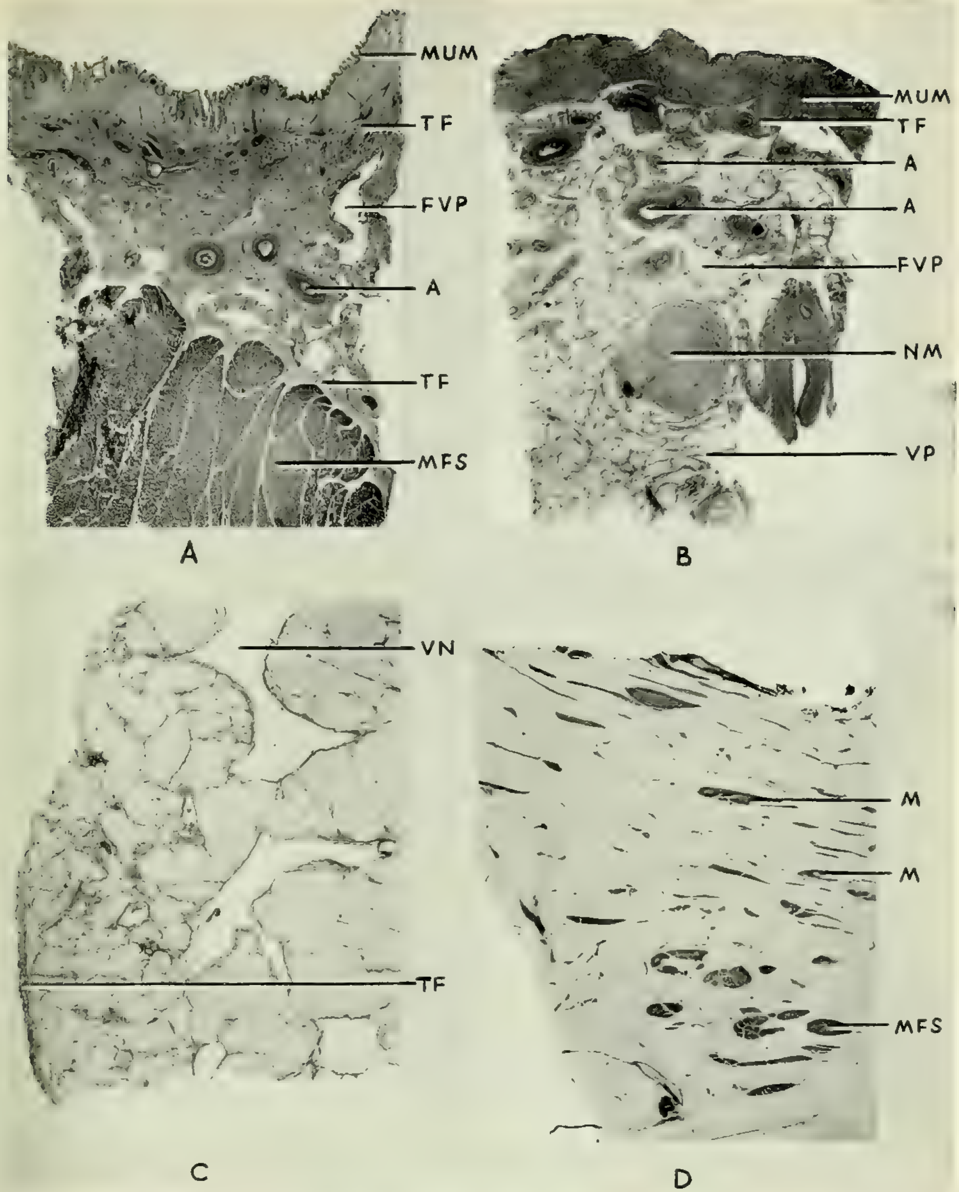
(A) Section at right angles to Plate 3, figure A (× 8).

(B) Section through lateral wall of the pterygoid sinus in the region anterior to the tympanic bulla (× 4).

(C) Transverse section of the intra-mandibular fatty body (× 8).

(D) Transverse section of fat external to mandible (× 8).

PLATE 4


MUM
TF
FVP
A
TF
MFS
A
MUM
TF
A
A
FVP
NM
VP
B
VN
TF
C
M
M
MFS
D

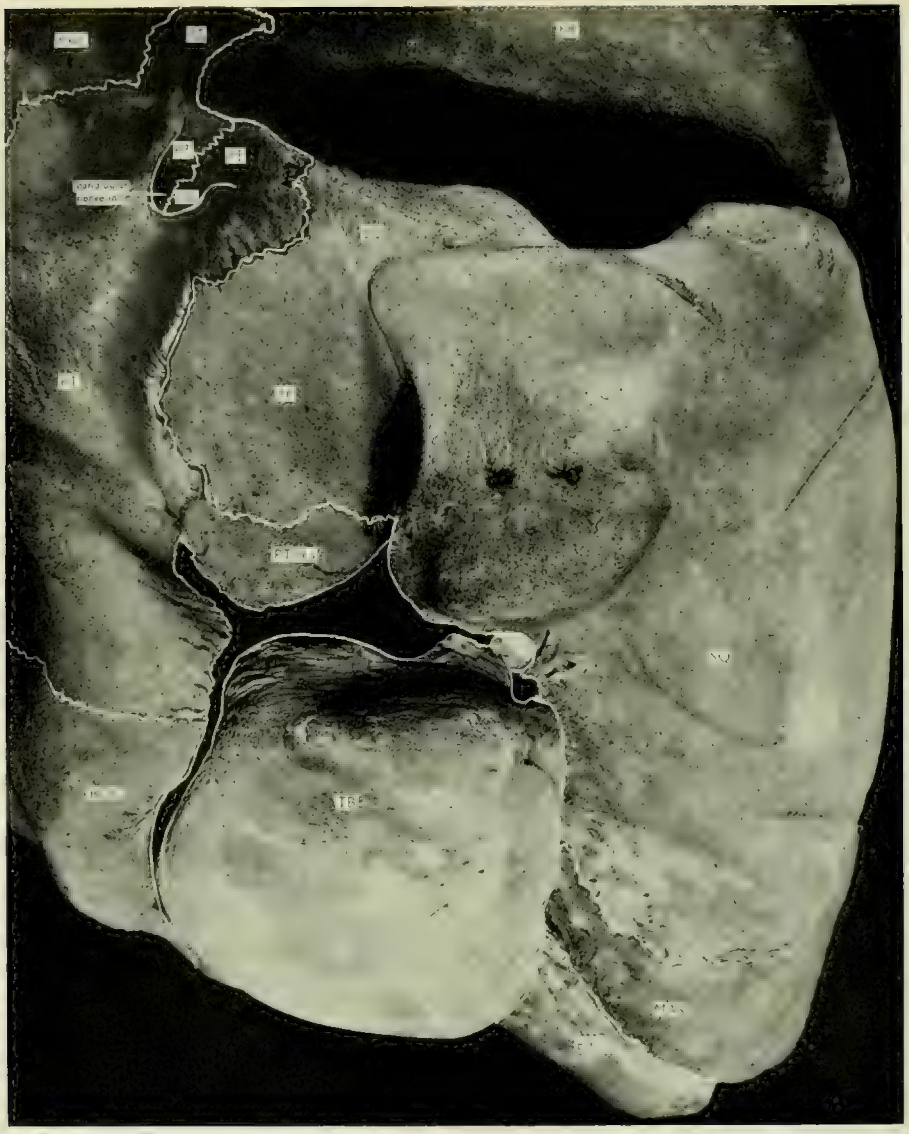


PLATE 5

Caperea marginata (Reg. No. 1876.2.16.1)
Ventral view of postero-lateral region of the skull, left side.

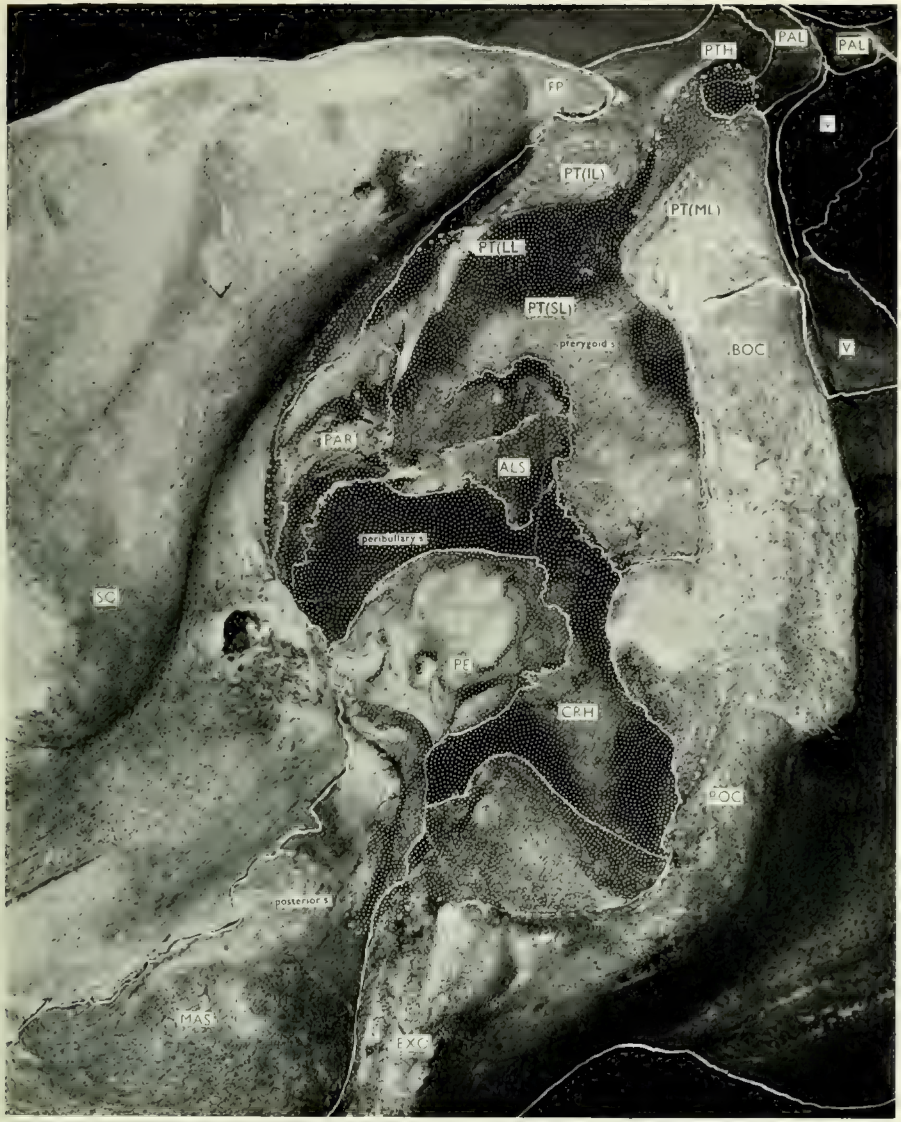

PTH
PAL
PAL
FP
PT(IL)
PT(ML)
PT(LL
PT(SL)
pterygoid s
BOC
V
PAR
ALS
peribullary s
SC
PE
CRH
BOC
posterior s
MAS
EXC

PLATE 6

Caperea marginata (Reg. No: 1876.2.16.1)
Ventral view of postero-lateral region of the skull, right side with tympanic bulla removed.

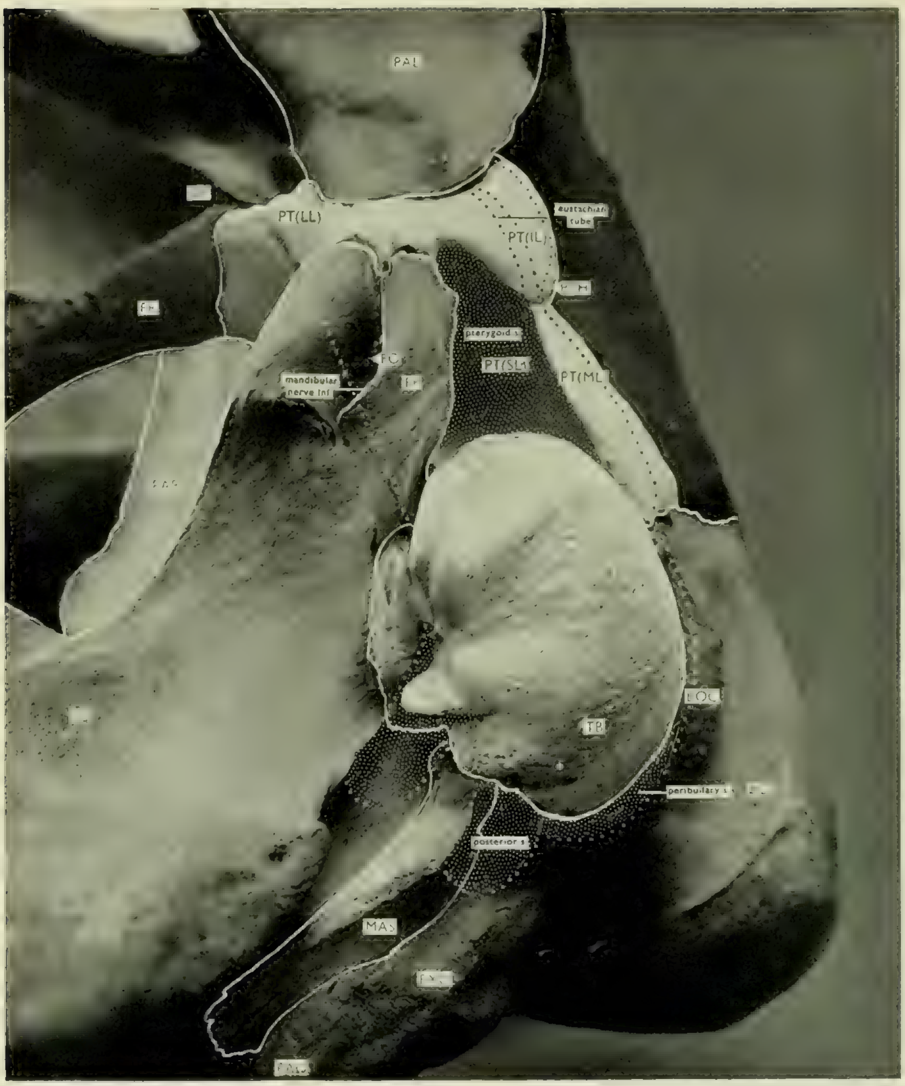

PAL
PT(LL)
eustachian tube
PT(IL)
FR
pterygoid s
PT(SL)
PT(ML)
FO
mandibular nerve inf
FR
TB
peribullary s
posterior s
MAS

PLATE 7

Balaenoptera acutorostrata (Reg. No. S.W. 1926/33)
Ventro-lateral view of the pterygoid and adjacent regions of the skull.

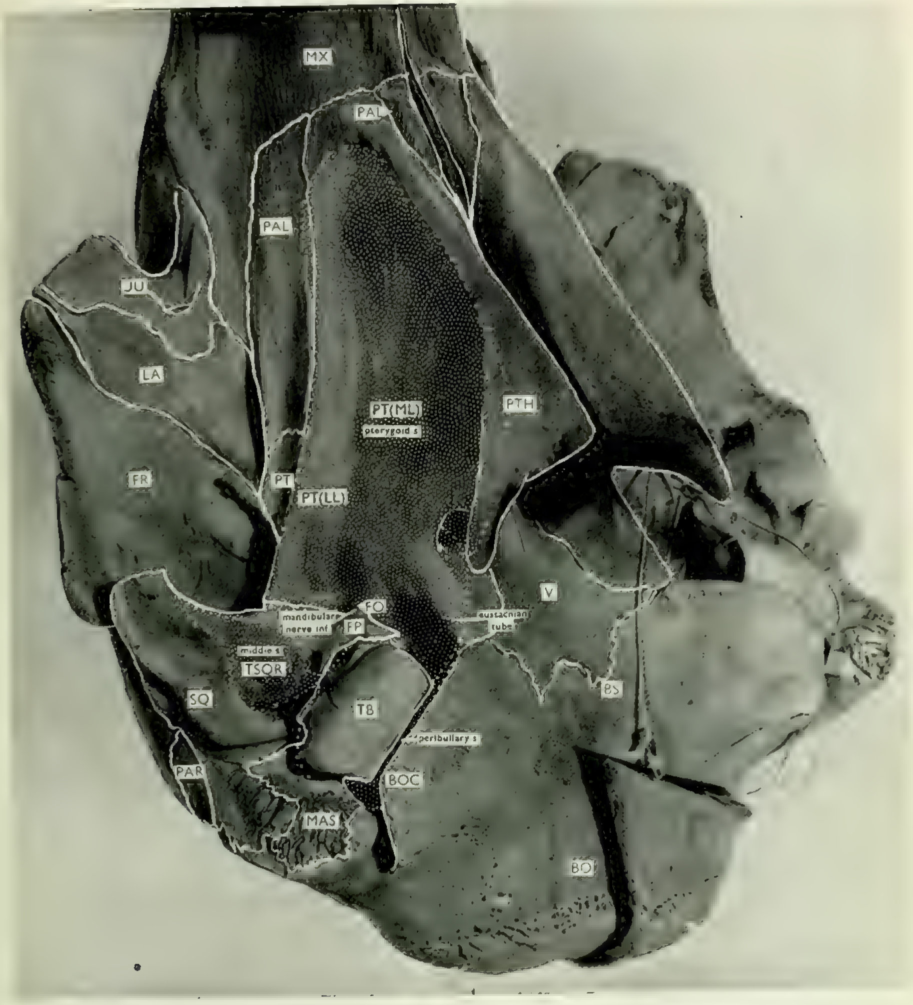

MX
PAL
PAL
JU
LA
FR
PT(ML)
pterygoid s
PTH
PT
PT(LL)
FO
mandibular nerve inf
FP
eustachian tube
V
middle s
TSQR
SQ
TB
BS
peribullary s
PAR
BOC
MAS
BO

PLATE 8

Hyperoodon ampullatus (Reg. No. S.W. 1938/40)
Ventro-lateral aspect of the skull base.

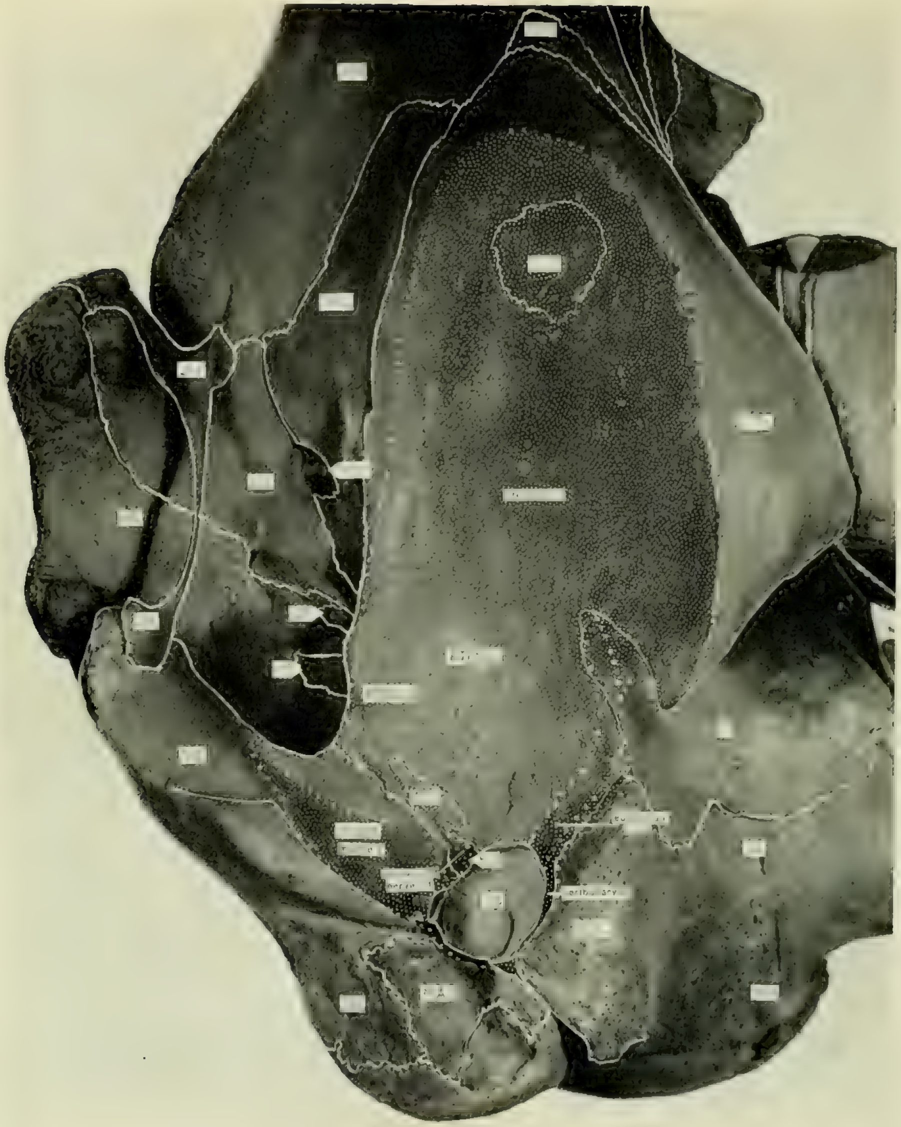


PLATE 9

Berardius arnuxi (Reg. No. 1923.11.16.1)
Ventro-lateral aspect of the skull base.

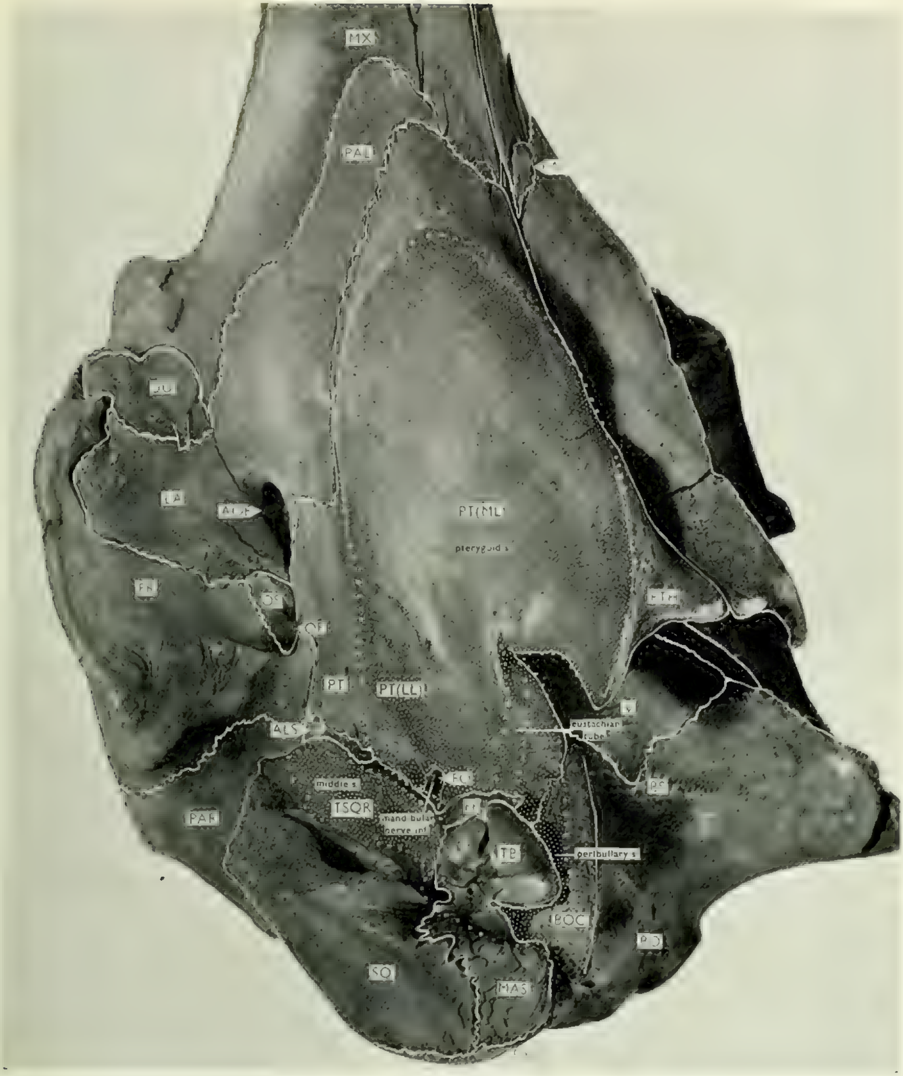

MX
PAL
LA
FN
PT(ML)
pterygoid s.
PT
PT(LL)
eustachian tube
ALS
middle s.
FO
TSQR
mandibular nerve inf
PAR
TB
peribullary s
BOC
SQ
MAS

PLATE 10

Ziphius cavirostris (Reg. No. 1920/9)
Ventro-lateral aspect of the skull base.

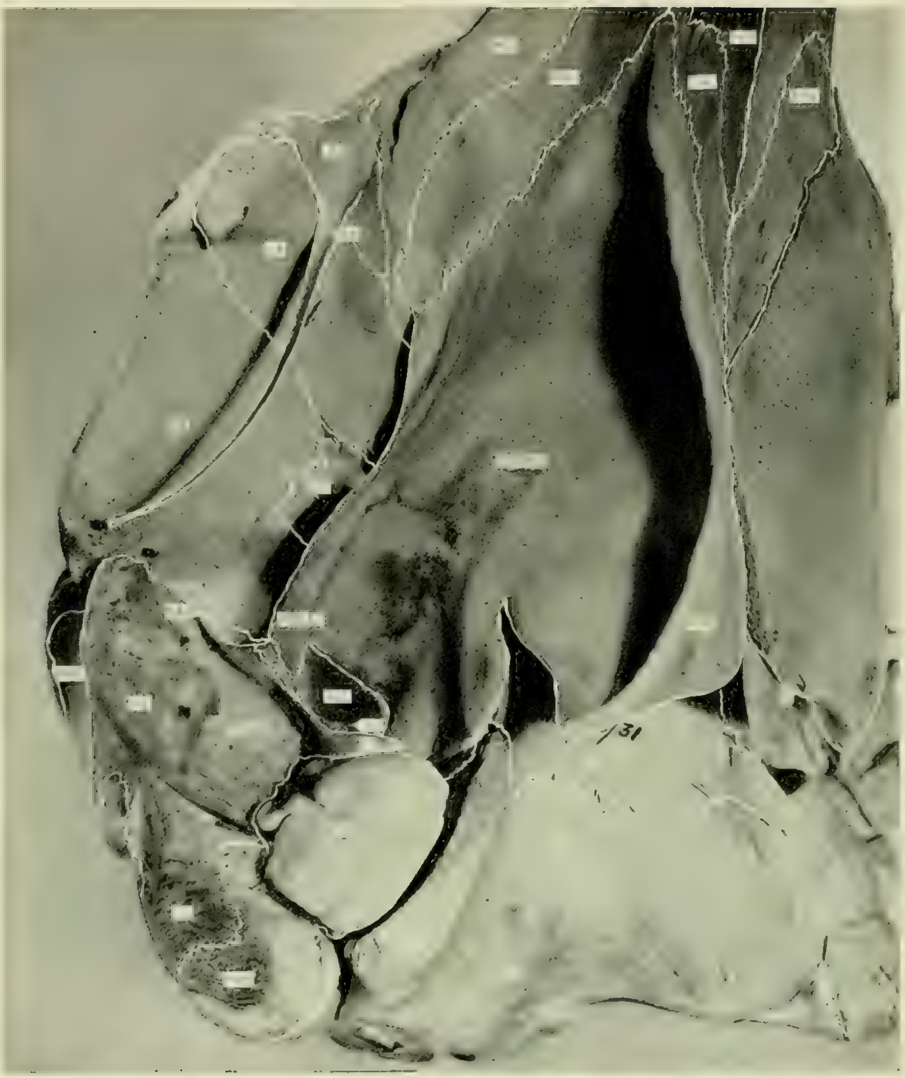


PLATE 11

Mesoplodon bidens (Reg. No. S.W.1938/31)
Ventro-lateral aspect of the skull base.

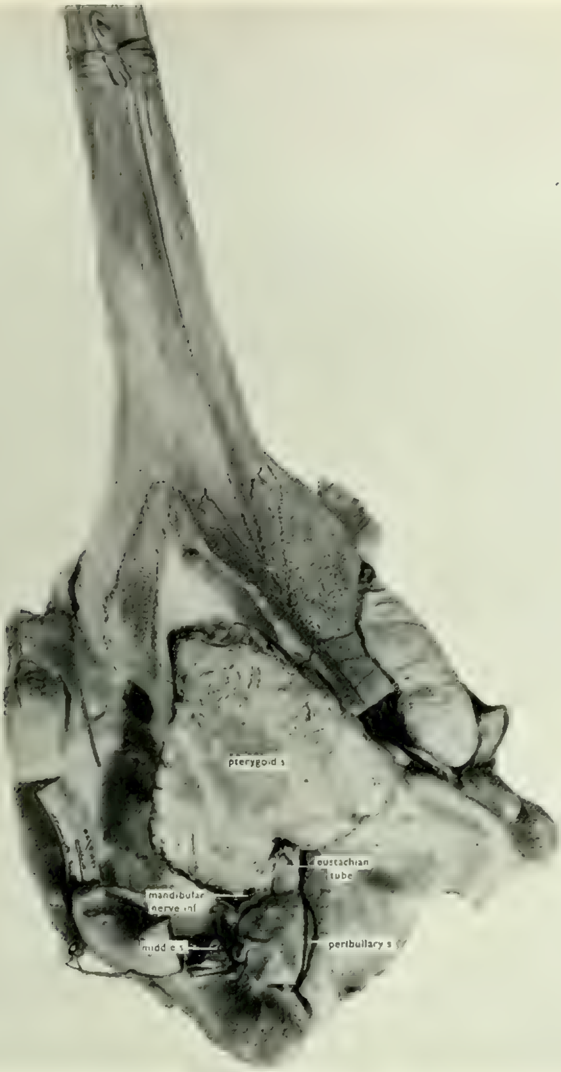

pterygoid s
eustachian tube
mandibular nerve inf
middle s
peribullary s

PLATE 12

Mesoplodon bidens (Reg. No. S.W. 1949/26)
Skull showing internal cast of air sinuses.

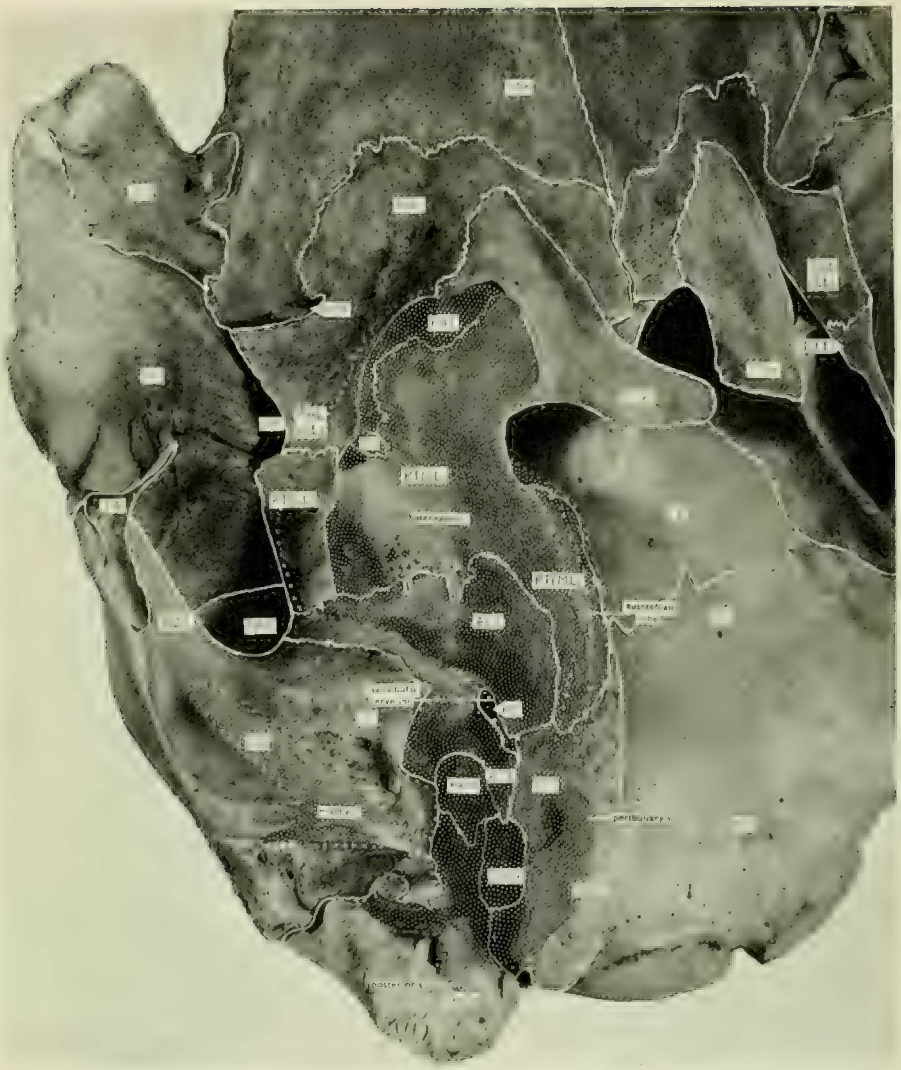

Pt.ML
peribullary s

PLATE 13

Monodon monoceros (Reg. No. 1949.11.2.1)
Base of skull of adult ventro-lateral aspect.

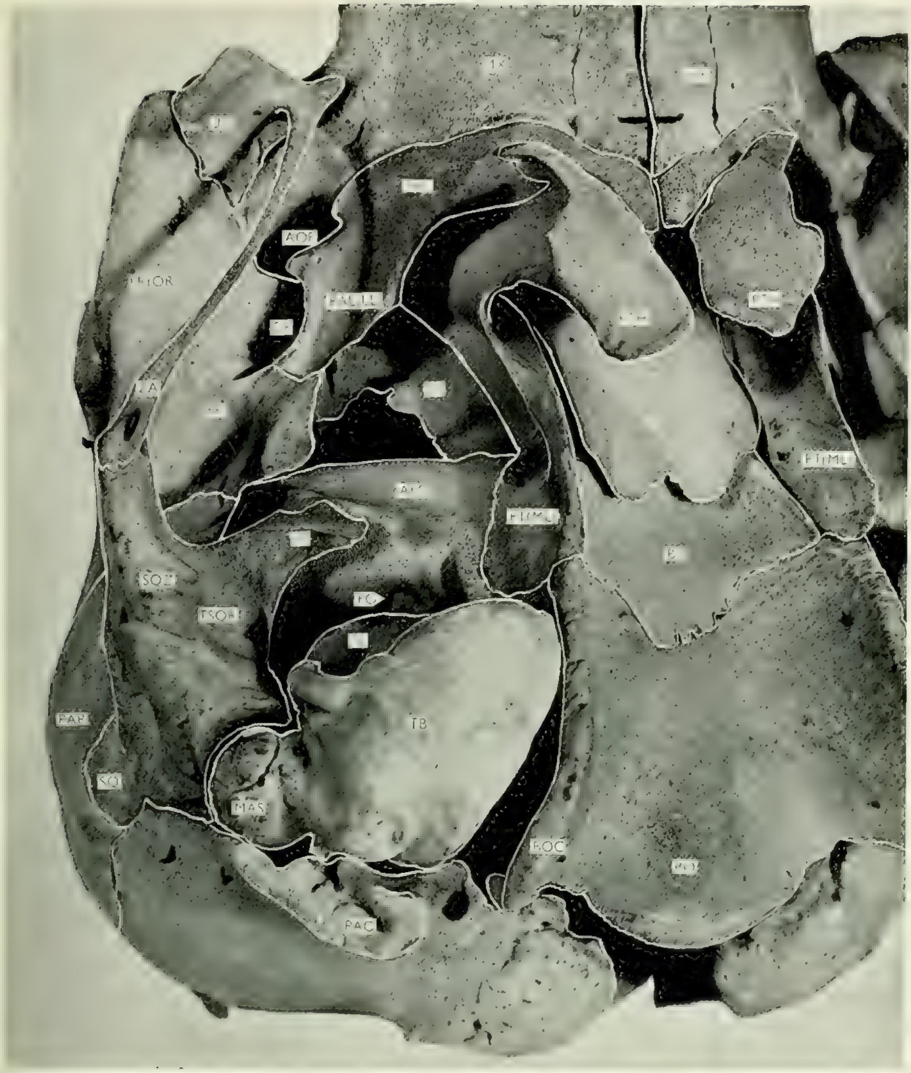

AOF
ZA
AL
SQ
TSQ
FO
PAR
SQ
TB
MAS
PAC
BOC
B

PLATE 14

Monodon monoceros juv. (Reg. No. 1887.9.8.1)
Ventro-lateral aspect of skull base.

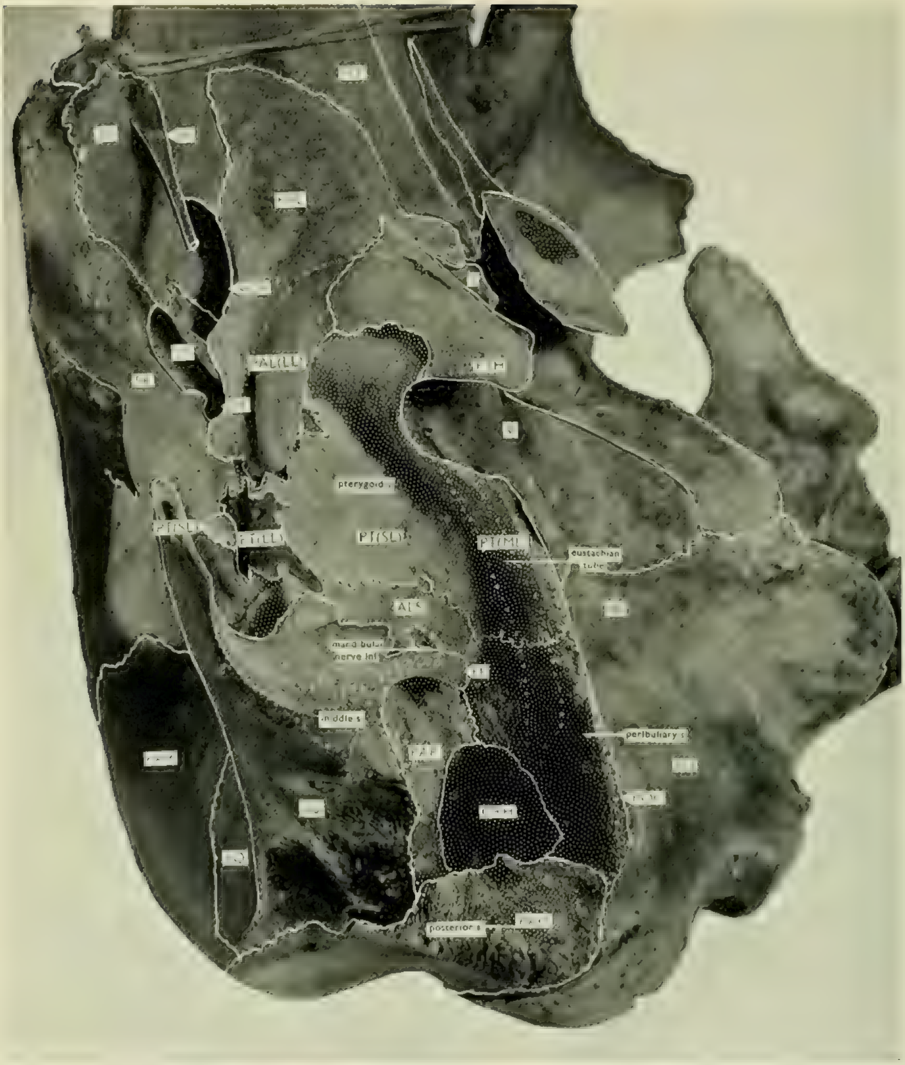

PAL(LL)
pterygoid
PT(SL)
PT(SL)
PT(LL)
PT(ML)
eustachian tube
AL
mand bulb nerve inf
middle s
peribullary s
posterior s

PLATE 15

Delphinapterus leucas (Reg. No. 1933.10.13.1)
Ventro-lateral aspect of skull base.

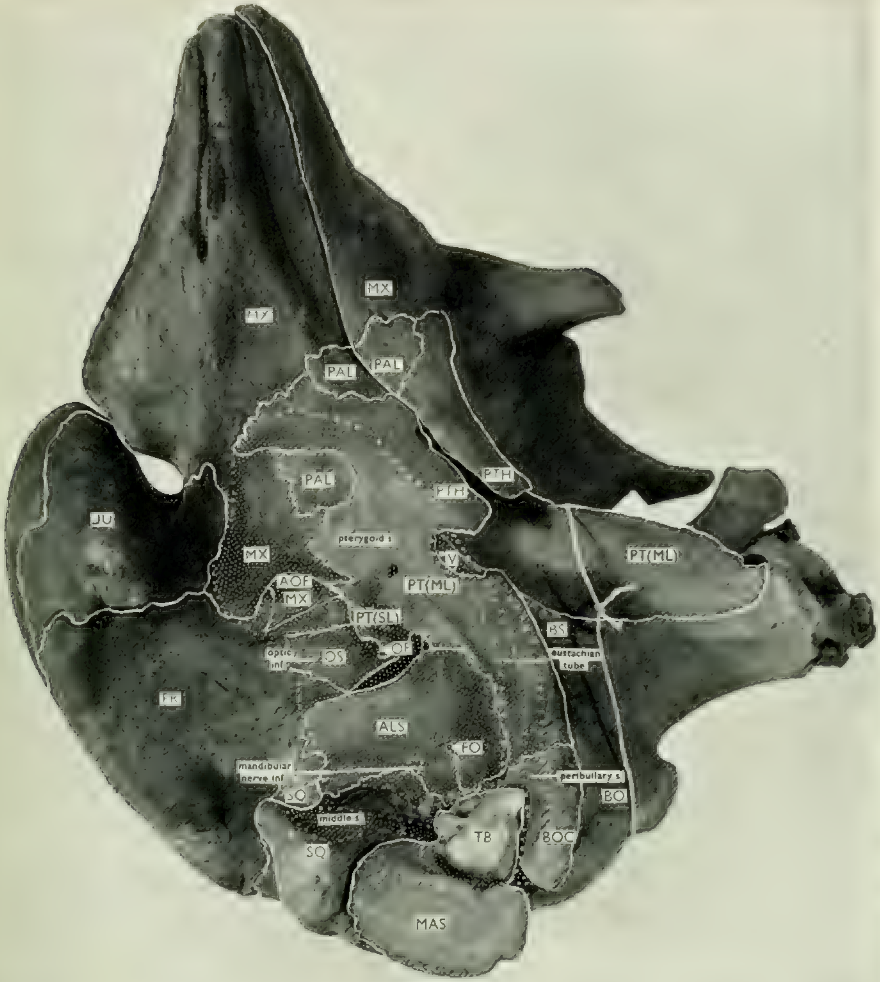

MX
MX
PAL
PAL
PTH
PAL
PTH
JU
pterygoid s
MX
V
AOF
PT(ML)
MX
PT(ML)
PT(SL)
BS
optic inf
OS
OF
eustachian tube
FR
ALS
FO
mandibular nerve inf
peribullary s
SQ
BO
middle s
TB
BOC
SQ
MAS

PLATE 16

Kogia breviceps (Reg. No. 1952.8.23.1)
Ventro-lateral aspect of the skull base.

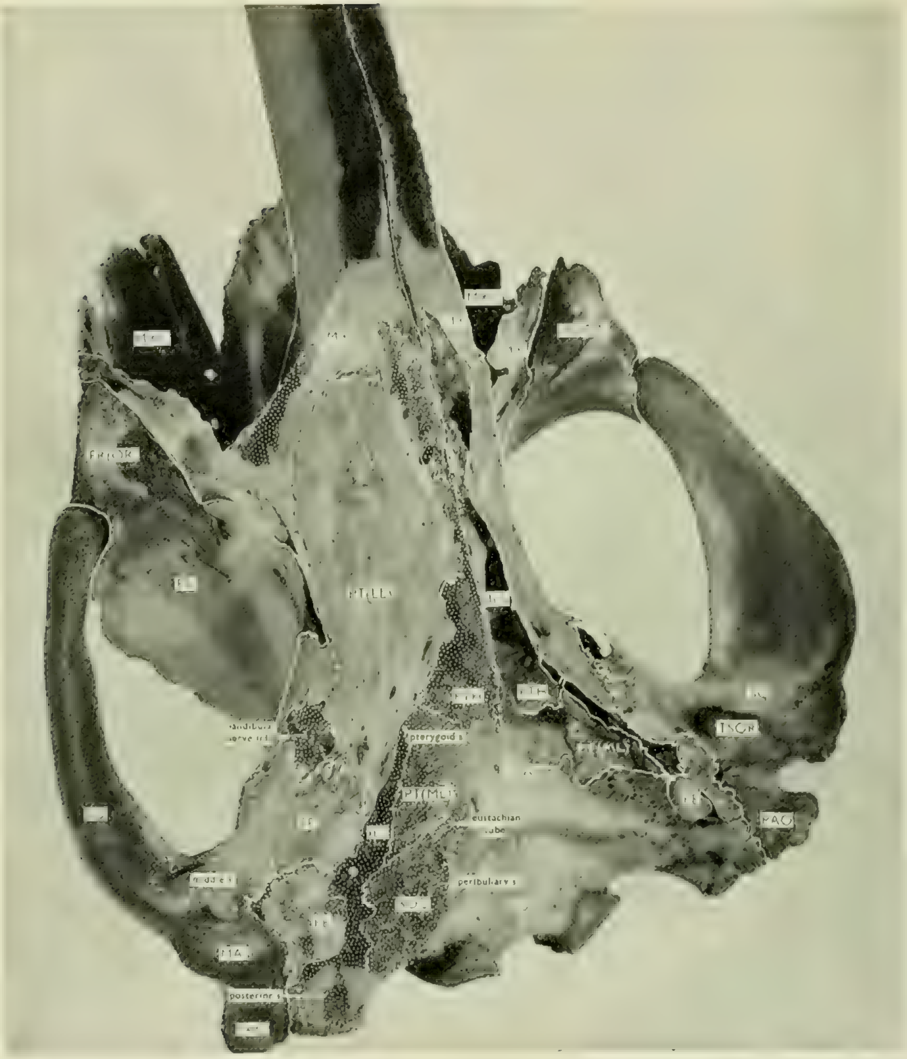

FR(OR)
PT(LL)
mandibular nerve
pterygoid s
PT(ML)
eustachian tube
TSQR
PAO
middle s
peribullary s
MA
posterior s

PLATE 17

Platanista gangetica, adult (Reg. No. 1843.8.18.5)
Ventro-lateral aspect of the skull base.

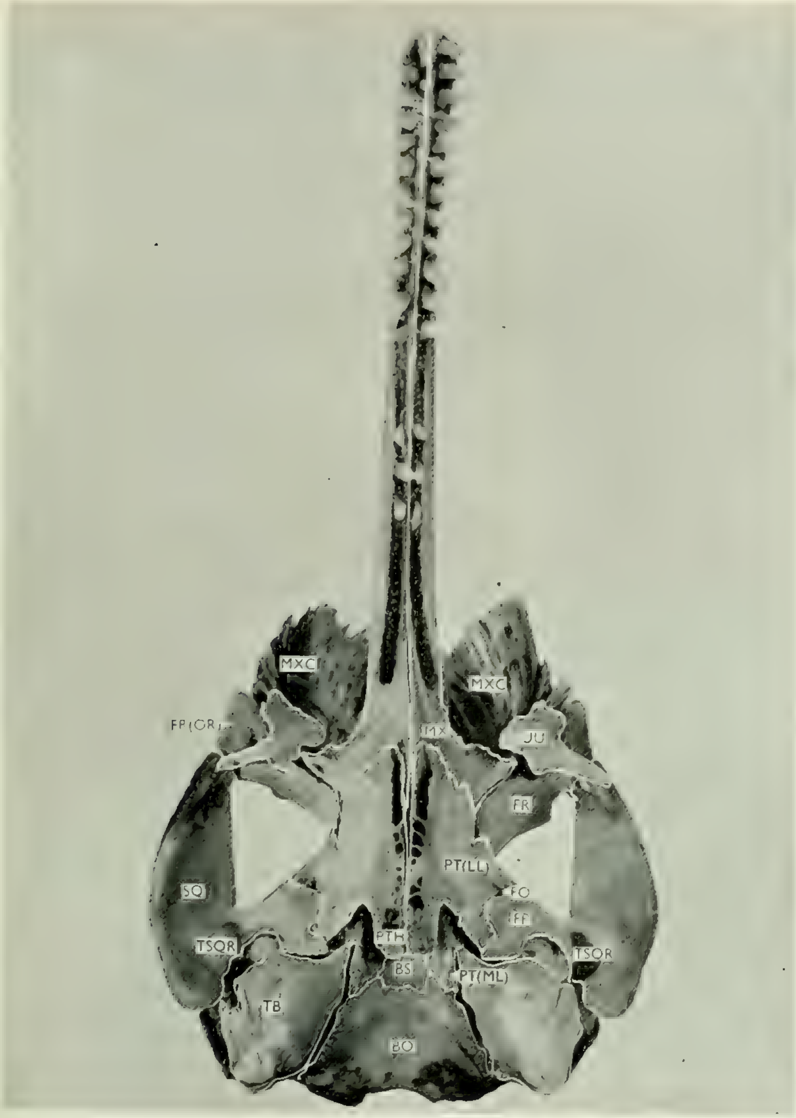

MXC
MXC
FP(OR)
MX
JU
FR
PT(LL)
SQ
FO
FF
TSQR
PTR
TSQR
BS
PT(ML)
TB
BO

PLATE 18

Platanista gangetica, juv. (Reg. No. 1646A)
Ventral aspect of skull.

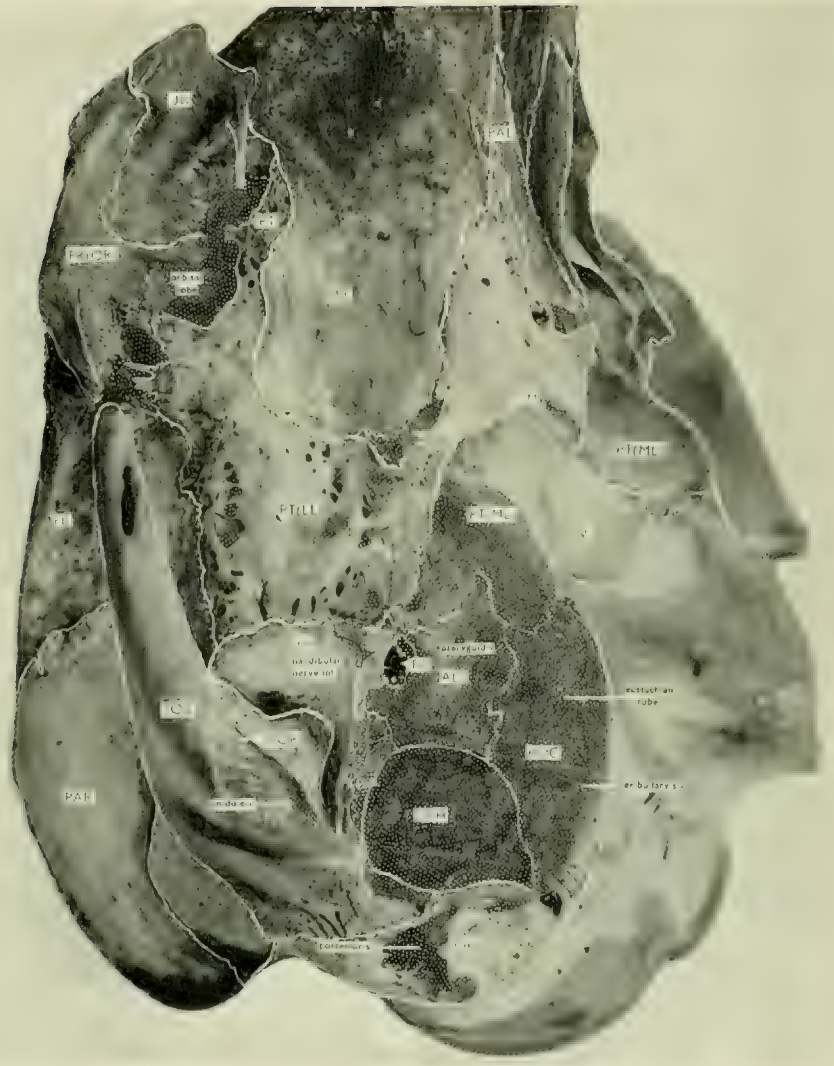

PAL
PT(LL)
PT(ML)
PT(ML)
AL
PAR
eustachian tube

PLATE 19

Stenodelphis blainvillei (Reg. No. 1925.11.20.1)
Ventro-lateral aspect of skull base.

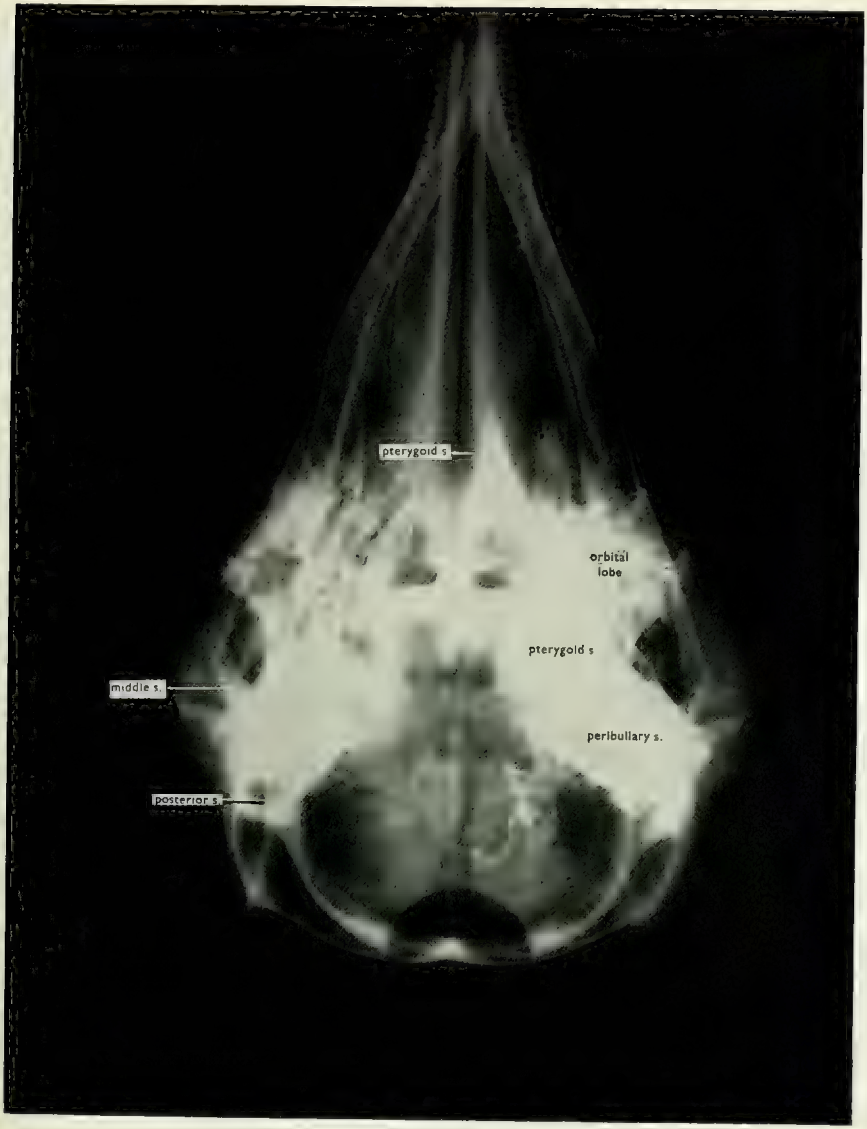

pterygoid s
orbital lobe
pterygoid s
middle s.
peribullary s.
posterior s.

PLATE 20

Stenodelphis blainvillei (no history)
Radiograph of head, sinuses injected with iodized oil.

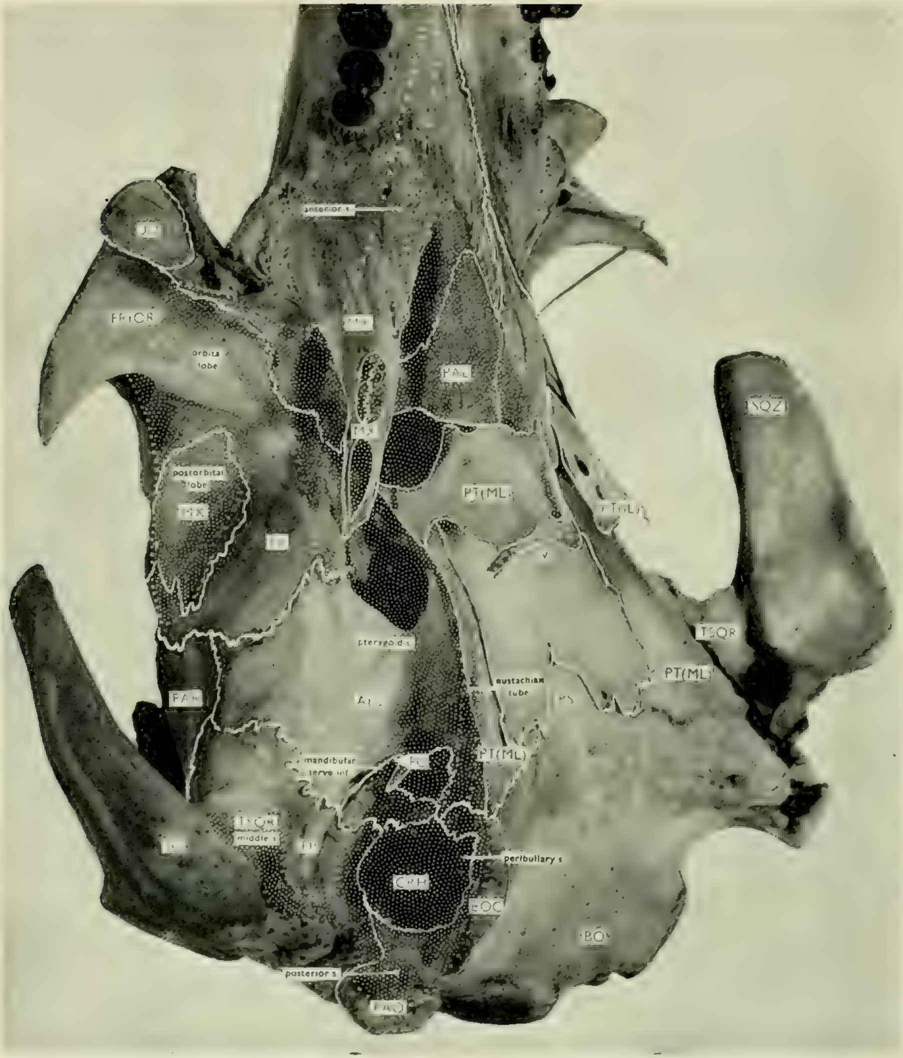

anterior s
FR(OR)
orbital lobe
PAL
MX
postorbital lobe
MX
PT(ML)
SQZ
pterygoid s
TSQR
PT(ML)
PAR
AL
eustachian tube
PS
mandibular nerve inf
PT(ML)
TSQR
middle s
peribullary s
CRH
EOC
BO
posterior s

PLATE 21

Inia geoffrensis (Reg. No. 1939.5.13.1)
Ventro-lateral aspect of skull base.

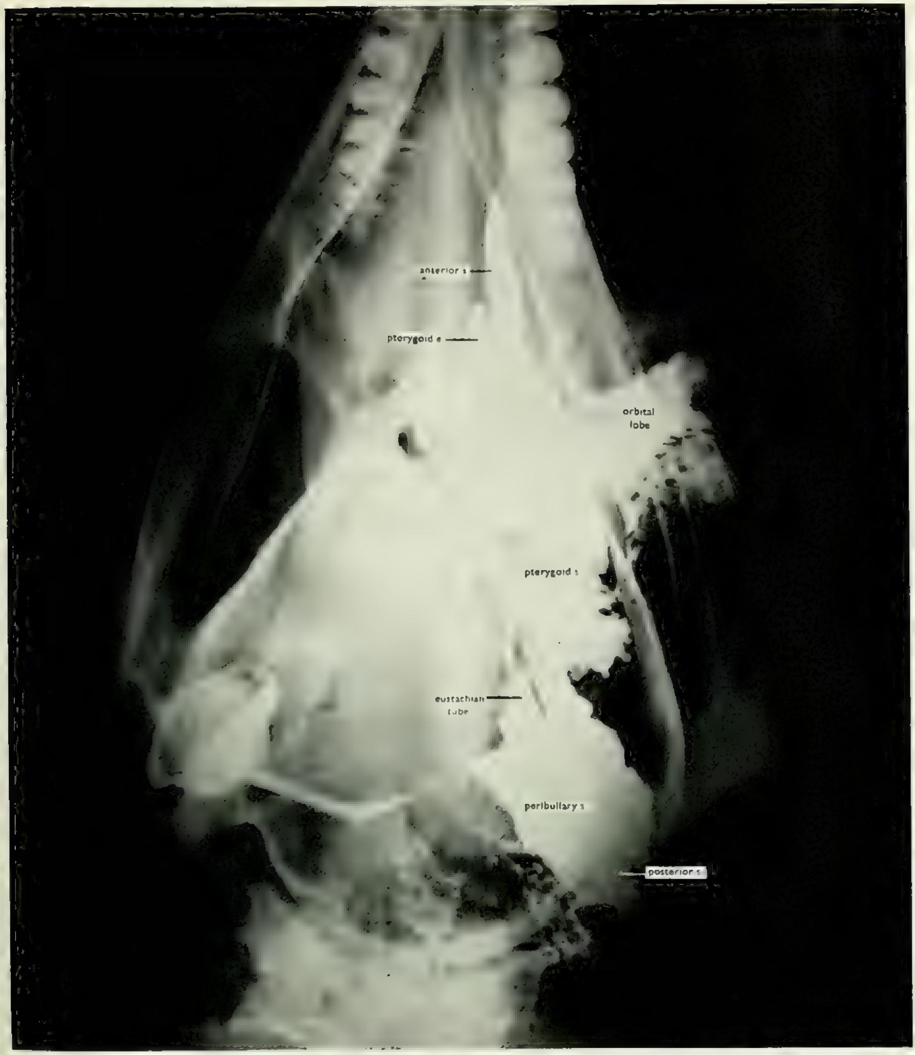

anterior s
pterygoid s
orbital lobe
pterygoid s
eustachian tube
peribullary s
posterior s

PLATE 22

Inia geoffrensis (Reg. No. 526.12.8.25)
Radiograph of head, sinuses of one side injected with iodized oil.

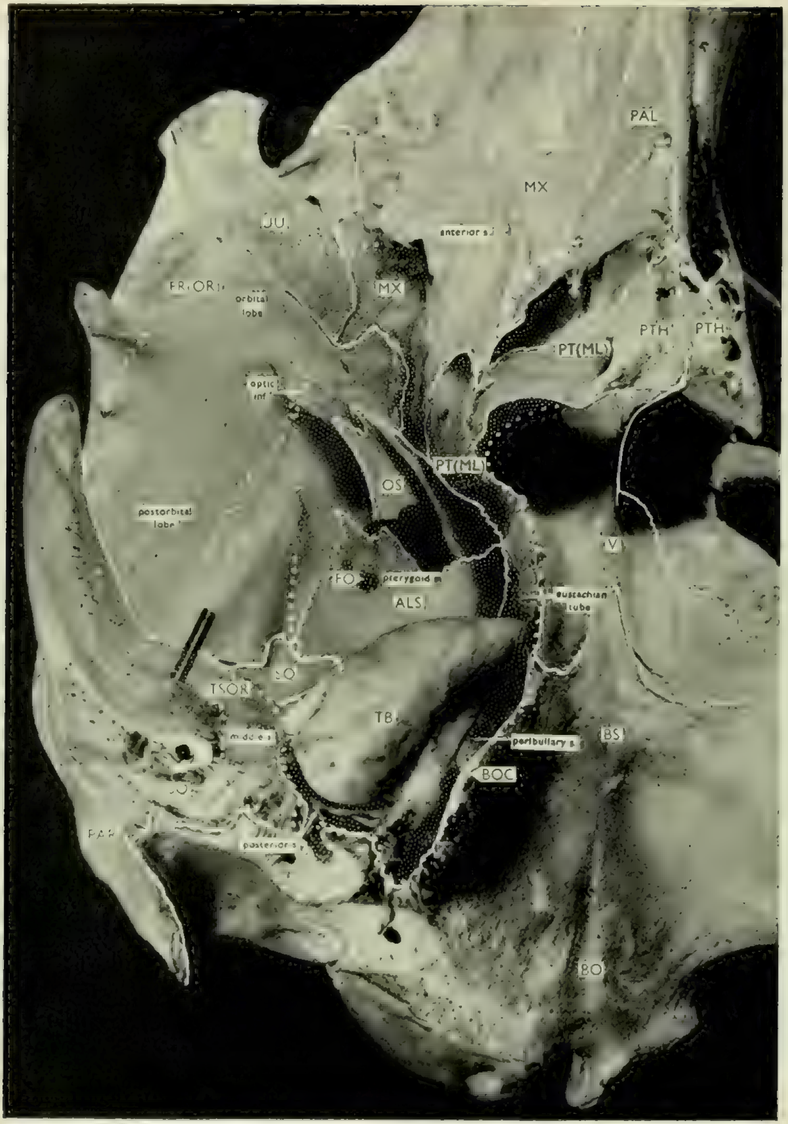

PAL
MX
JU
anterior s.
FR(OR)
orbital lobe
MX
PTH
PTH
PT(ML)
optic inf.
PT(ML)
OS
postorbital lobe
V
FO
pterygoid m.
ALS
eustachian tube
SQ
TSOR
TB
middle s.
peribullary s.
BS
BOC
PAR
posterior s.
BO

PLATE 23

Lipotes vexillifer (Reg. No. 22.6.22.1)

Ventro-lateral aspect of skull base.

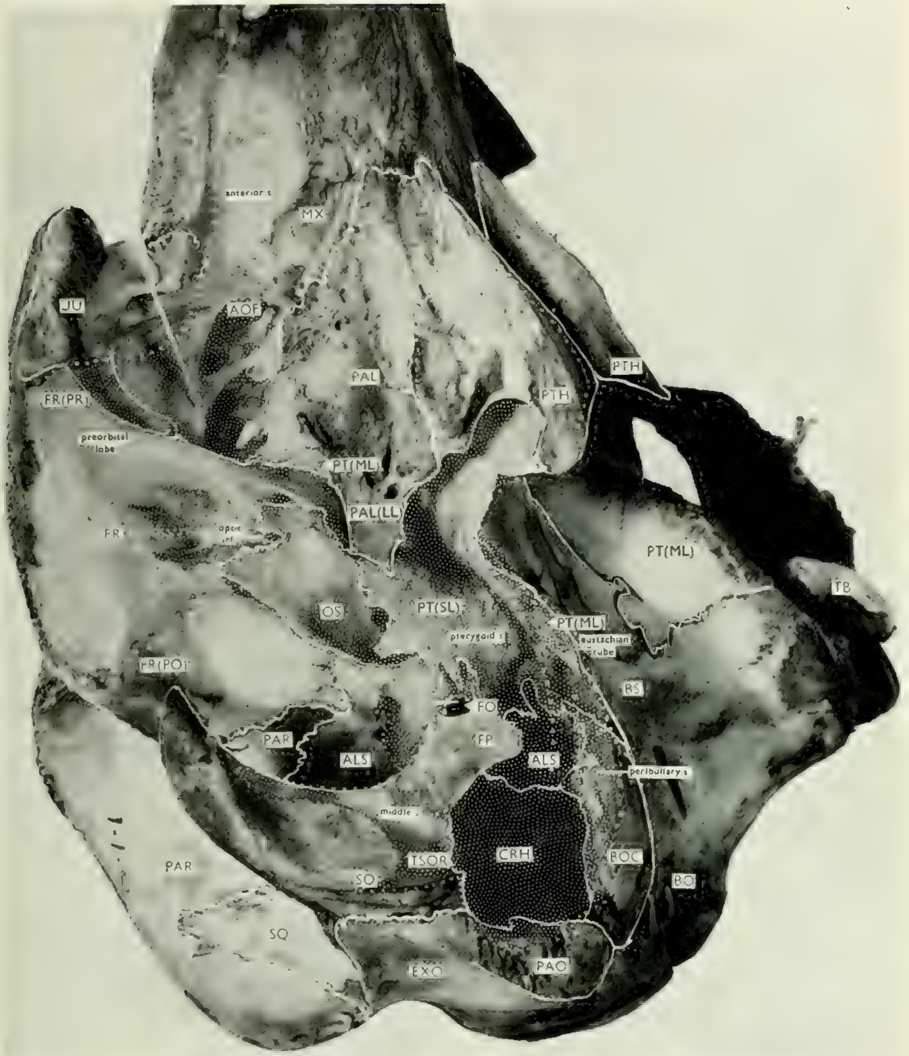

anterior s
MX
JU
AOF
PAL
PTH
PTH
FR(PR)
preorbital lobe
PT(ML)
PAL(LL)
FR
optic inf
PT(ML)
TB
OS
PT(SL)
PT(ML)
pterygoid s
eustachian tube
FR(PO)
BS
FO
PAR
FP
ALS
ALS
peribullary s
middle
CRH
BOC
TSOR
SO
BO
PAR
SQ
EXO
PAO

PLATE 24

Steno bredanensis (Reg. No. 1952.8.1.1)
Ventro-lateral aspect of skull base.

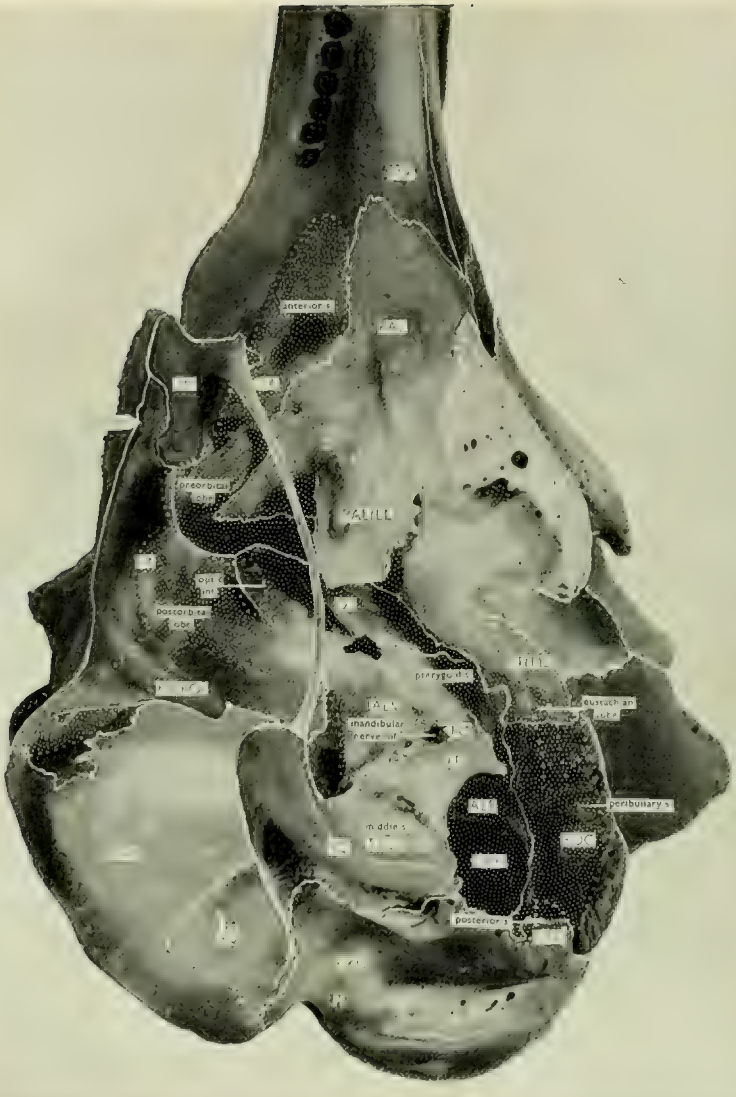

anterior s
preorbital
lobe
MAXILL
opt c
inf
postorbital
lobe
pterygoid s
eustachian
tube
mandibular
nerve inf
middle s
peribullary s
posterior s

PLATE 25

Sousa borneensis (Reg. No. 1914.1.14.1)
Ventro-lateral aspect of skull base.

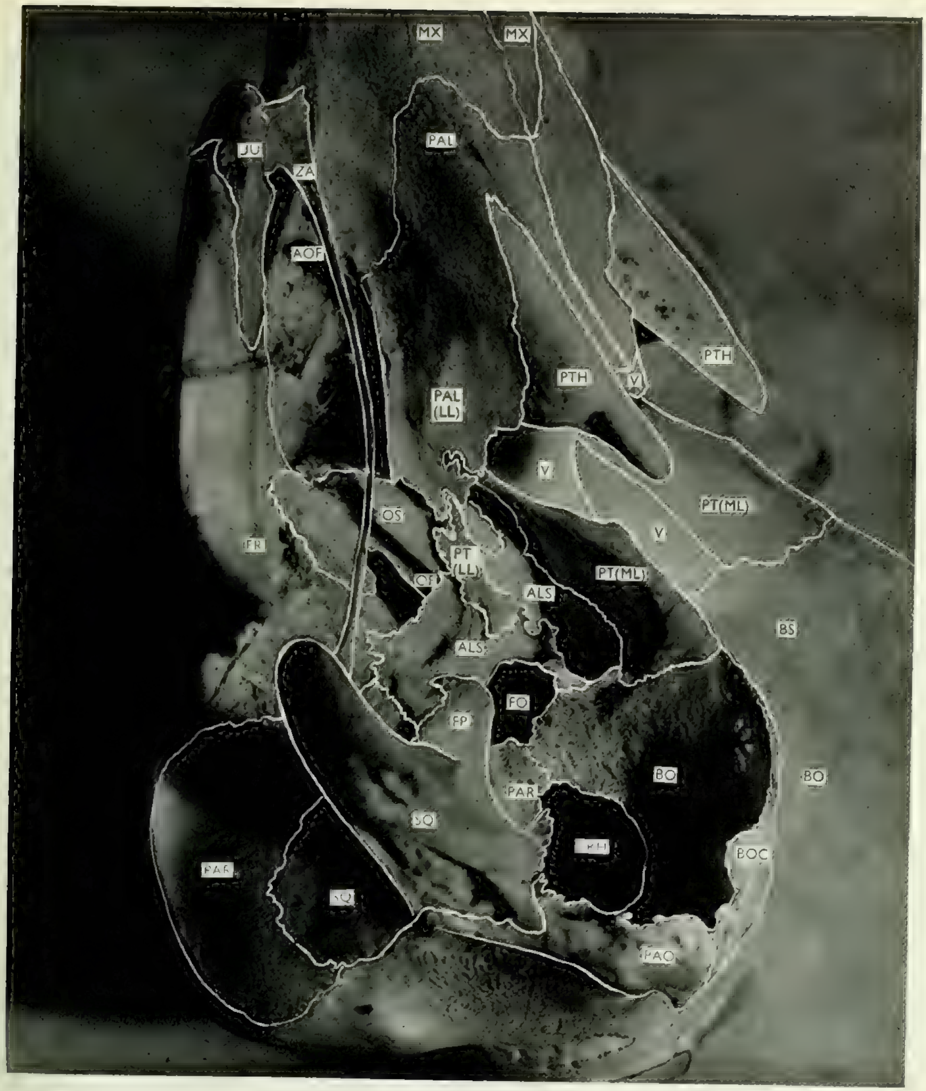

MX
MX
PAL
JU
ZA
AOF
PTH
PTH
V
PAL (LL)
V
PT(ML)
OS
FR
V
PT (LL)
CF
PT(ML)
ALS
BS
ALS
FO
FP
BO
BO
PAR
SQ
RH
BOC
PAR
SQ
PAO

PLATE 26

Phocaena phocoena (Reg. No. S.W. 1950/15)
Ventro-lateral aspect of skull base.

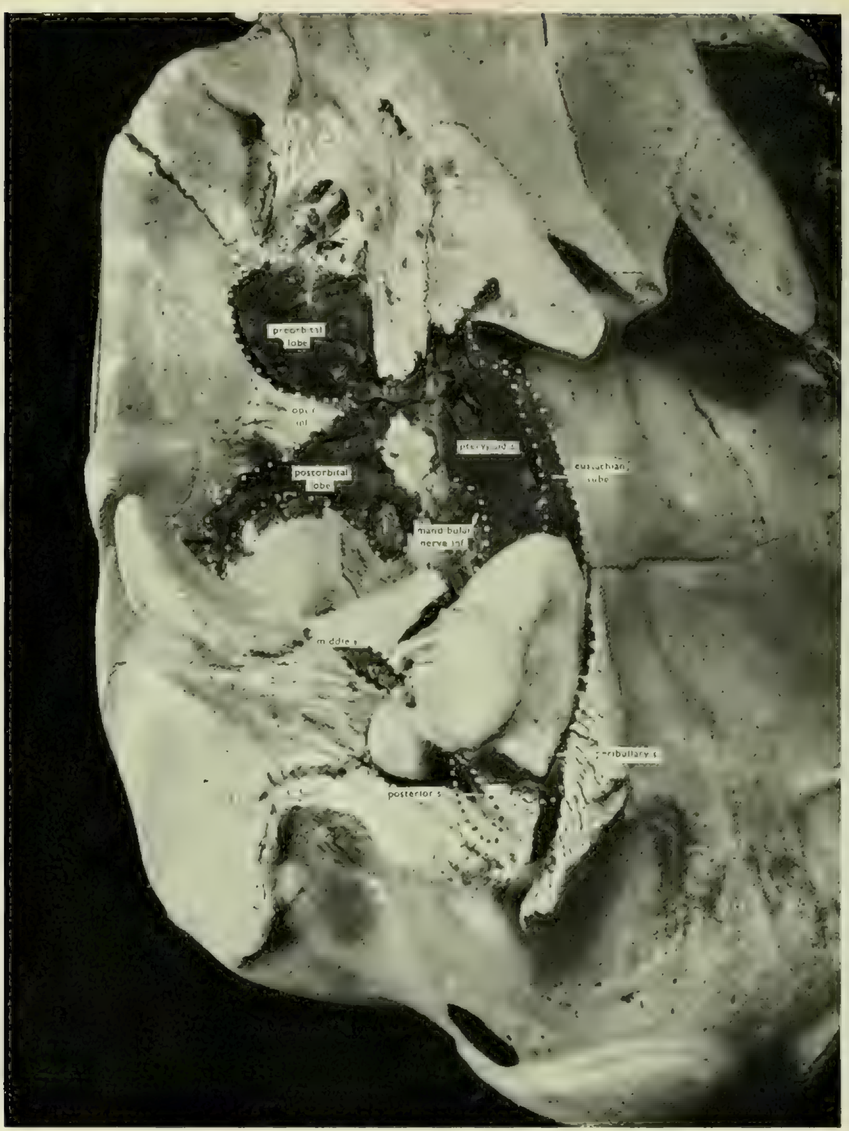

preorbital lobe
opt f
inf
pterygoid s
eustachian tube
postorbital lobe
mandibular nerve inf
middle s
peribullary s
posterior s

PLATE 27

Phocaena phocoena (Reg. No. S.W.1950/28)
Skull showing internal cast of air sinuses.

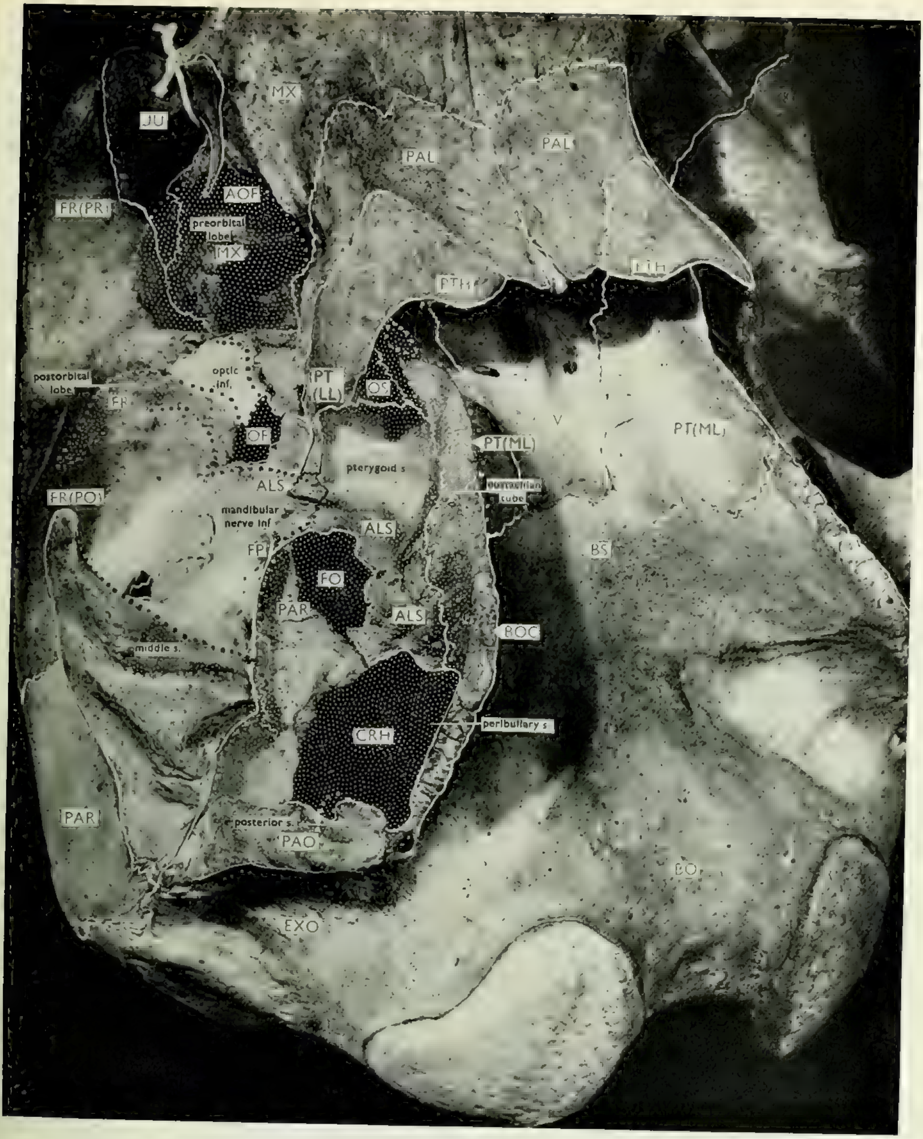

JU
MX
PAL
PAL
AOF
FR(PR)
preorbital lobe
MX
PTH
PTH
PT (LL)
OS
optic inf.
postorbital lobe
FR
OF
V
PT(ML)
PT(ML)
pterygoid s
ALS
eustachian tube
FR(PO)
mandibular nerve inf
ALS
FP
BS
FO
PAR
ALS
BOC
middle s.
CRH
peribullary s.
PAR
posterior s.
PAO
BO
EXO

PLATE 28

Neomeris phocaenoides (Reg. No. 1903.9.12.3)
Ventro-lateral aspect of skull base.

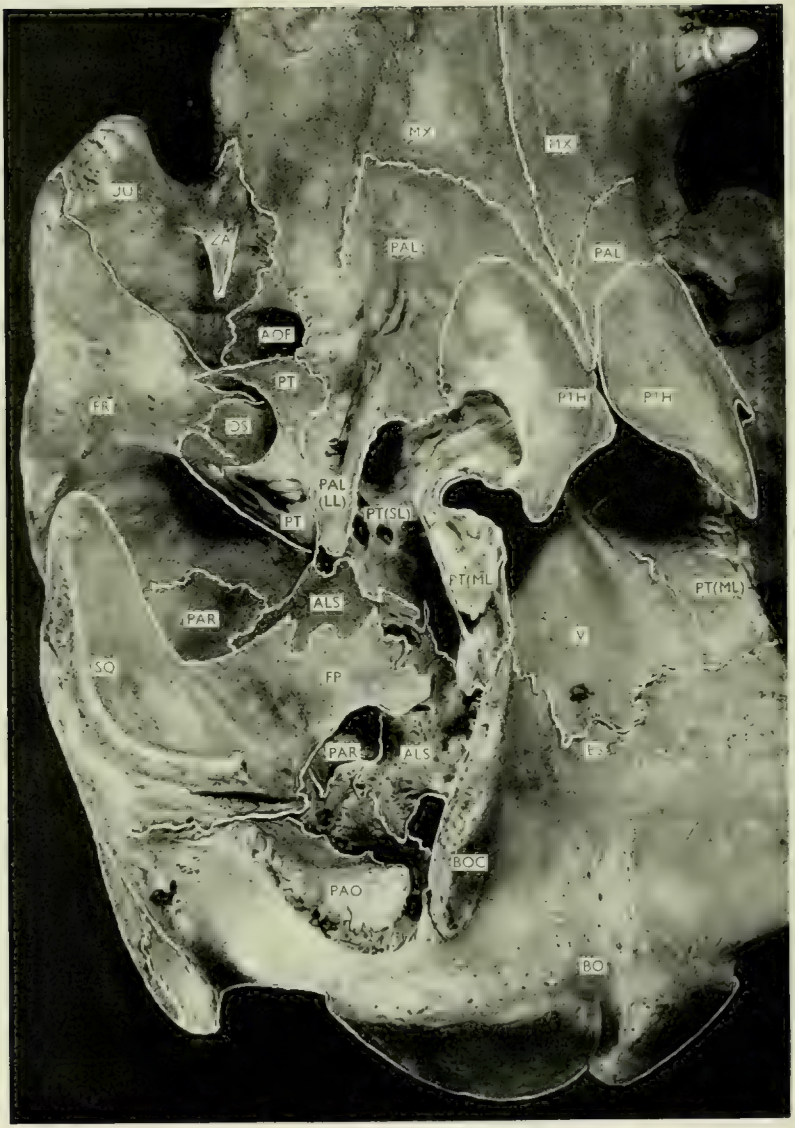

MX
MX
JU
ZA
PAL
PAL
AOF
PT
FR
OS
PTH
PTH
PAL (LL)
PT(SL)
PT
PT(ML)
PT(ML)
ALS
PAR
V
SQ
FP
PAR
ALS
ES
BOC
PAO
BO

PLATE 29

Pseudorca crassidens (Reg. No. S.W.1927/31)
Ventro-lateral aspect of skull base.

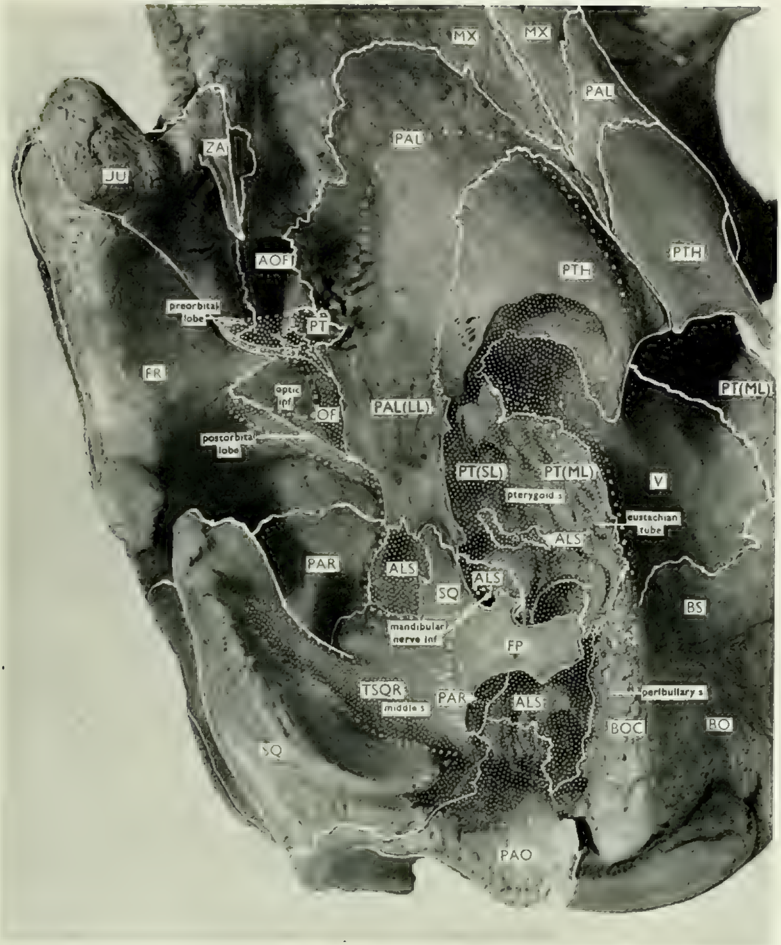

MX
MX
PAL
PAL
ZA
JU
PTH
PTH
AOF
preorbital lobe
PT
FR
PT(ML)
optic inf
OF
PAL(LL)
postorbital lobe
PT(SL)
PT(ML)
pterygoid s
V
eustachian tube
ALS
PAR
ALS
SQ
ALS
BS
mandibular nerve inf
FP
TSQR
PAR
ALS
peribullary s
middle s
BOC
BO
SQ
PAO

PLATE 30

Pseudorca crassidens (Reg. No. 1936.6.23.1)
Ventro-lateral aspect of skull base (for comparison with Plate 29).

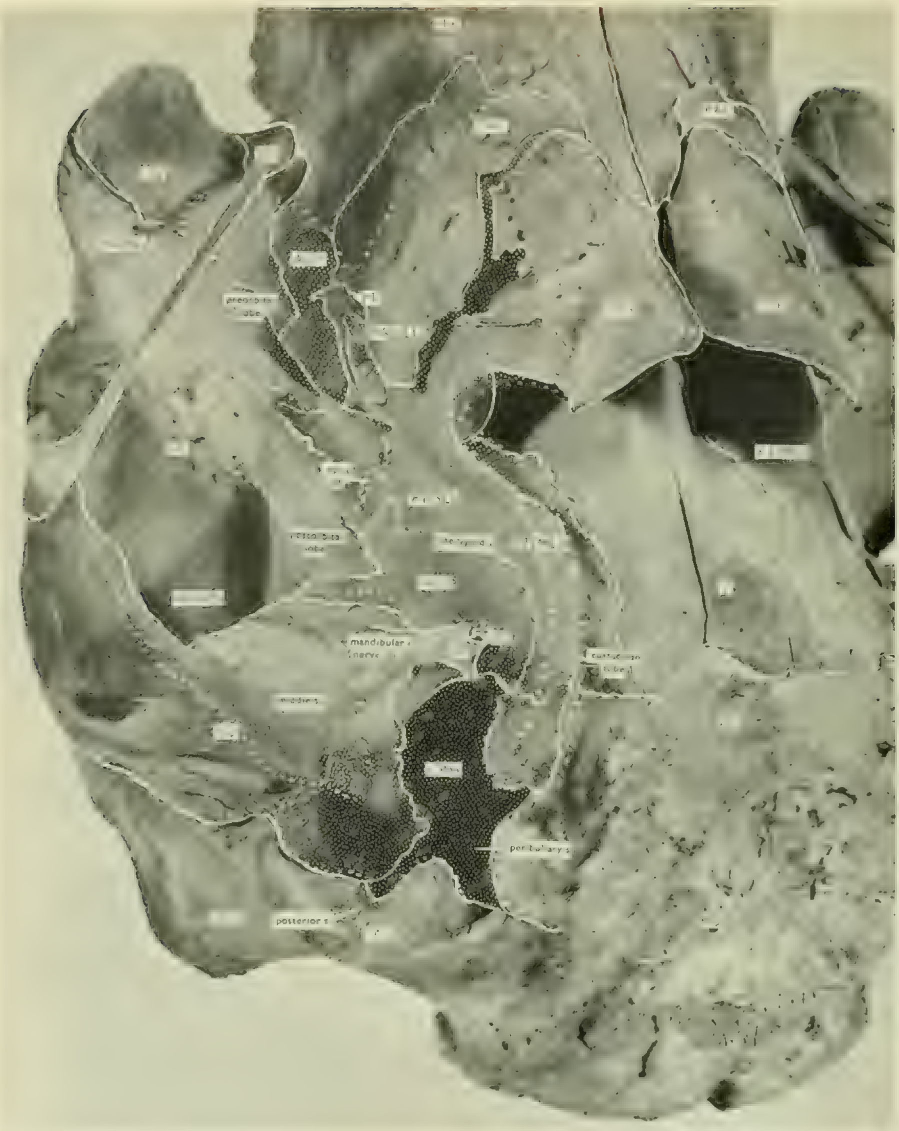

preorbital lobe
postorbital lobe
pterygoid
mandibular nerve
middle s
peribullary s
posterior s

PLATE 31

Orcinus orca (Reg. No. S.W. 1932/13)
Ventro-lateral aspect of skull base.

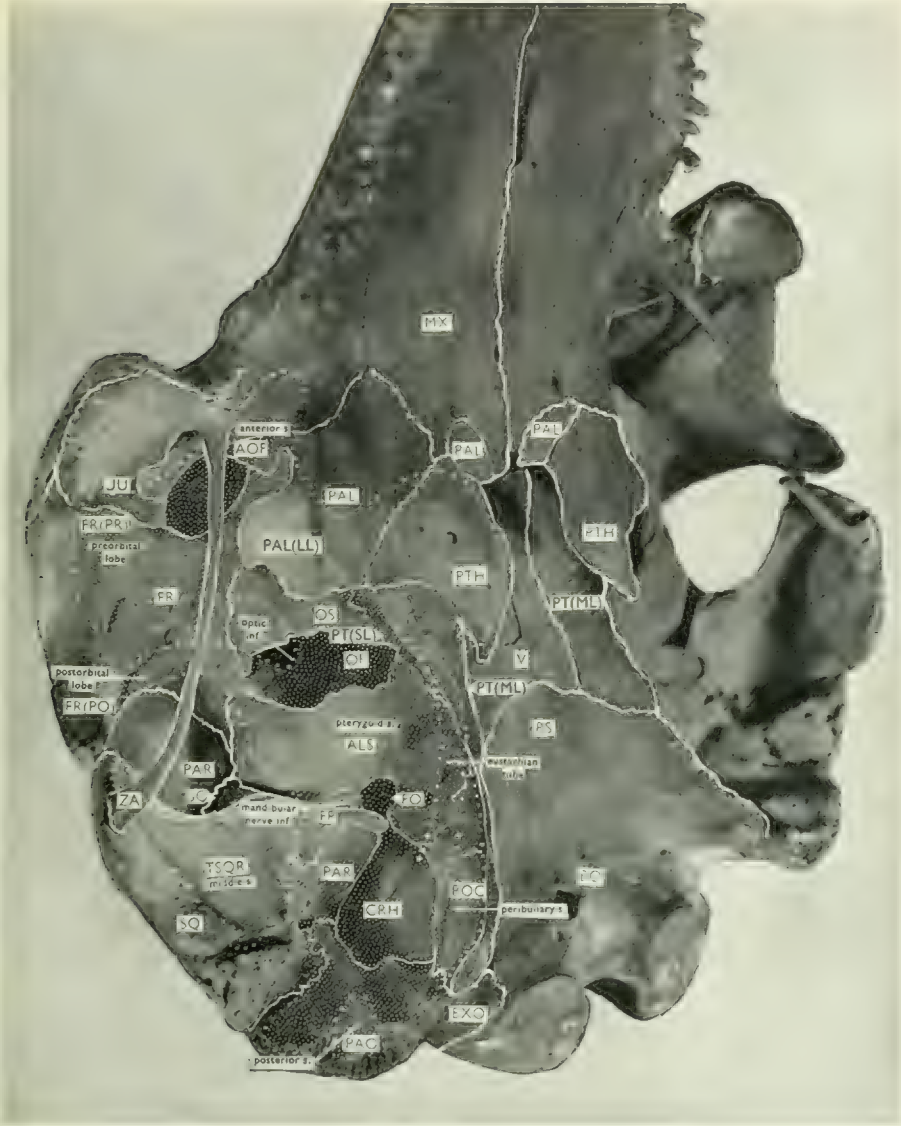

MX
anterior s.
AOF
PAL
PAL
PAL
JU
FR(PR)
preorbital lobe
PAL(LL)
PTH
PTH
PT(ML)
FR
OS
optic inf
PT(SL)
OF
V
PT(ML)
postorbital lobe
FR(PO)
pterygoid s.
ALS
PS
eustachian tube
PAR
ZA
GC
mandibular nerve inf
FP
FO
TSQR
middle s.
PAR
POC
LC
CRH
peribullary s.
SQ
EXO
PAC
posterior s.

PLATE 32

Orcaella brevirostris (Reg. No. 1883.11.20.2)
Ventro-lateral aspect of skull base.

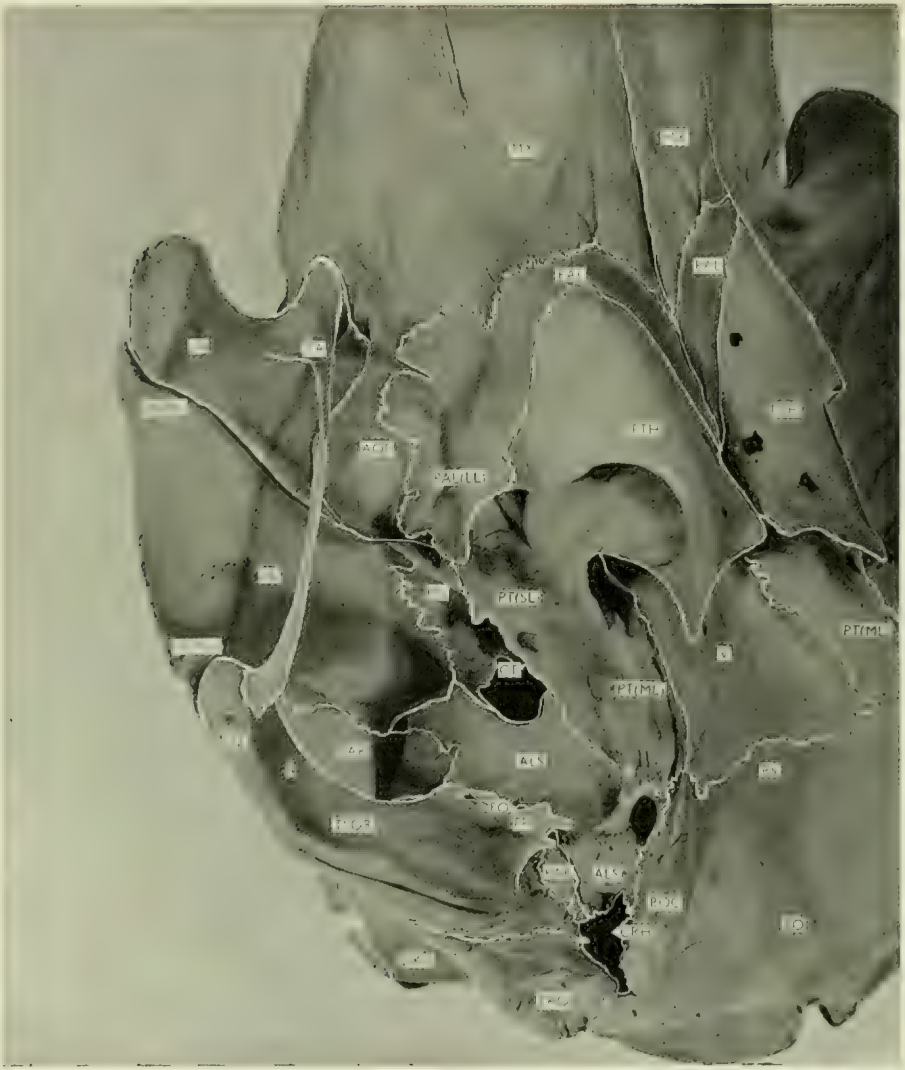

MX
AOF
PAL(LL)
PTH
PT(SL)
PT(ML)
CF
PT(ML)
ALS
ALS
BOC
CRH

PLATE 33

Globicephala melaena (Reg. No. S.W.1932/1)
Ventro-lateral aspect of skull base.

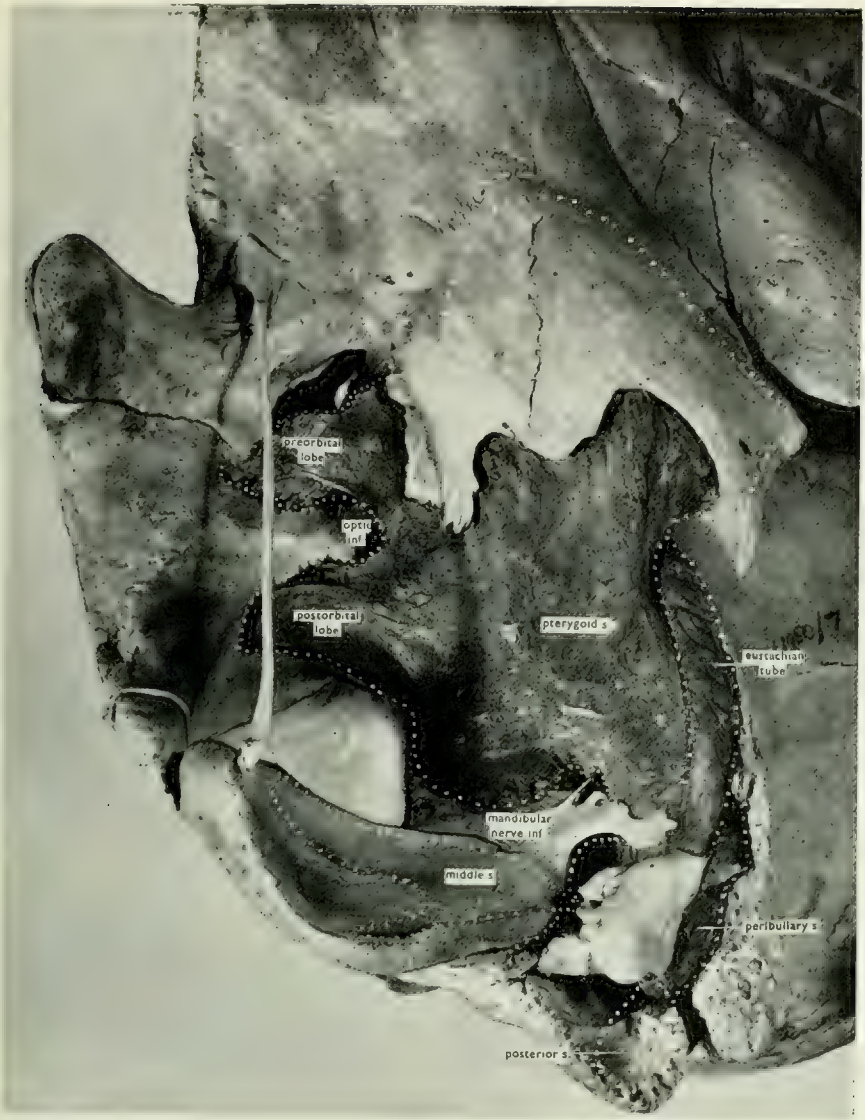

preorbital lobe
optic inf
postorbital lobe
pterygoid s
eustachian tube
mandibular nerve inf
middle s
peribullary s
posterior s.

PLATE 34

Globicephala melaena (Reg. No. 1950/7)
Skull showing internal cast of air sinuses

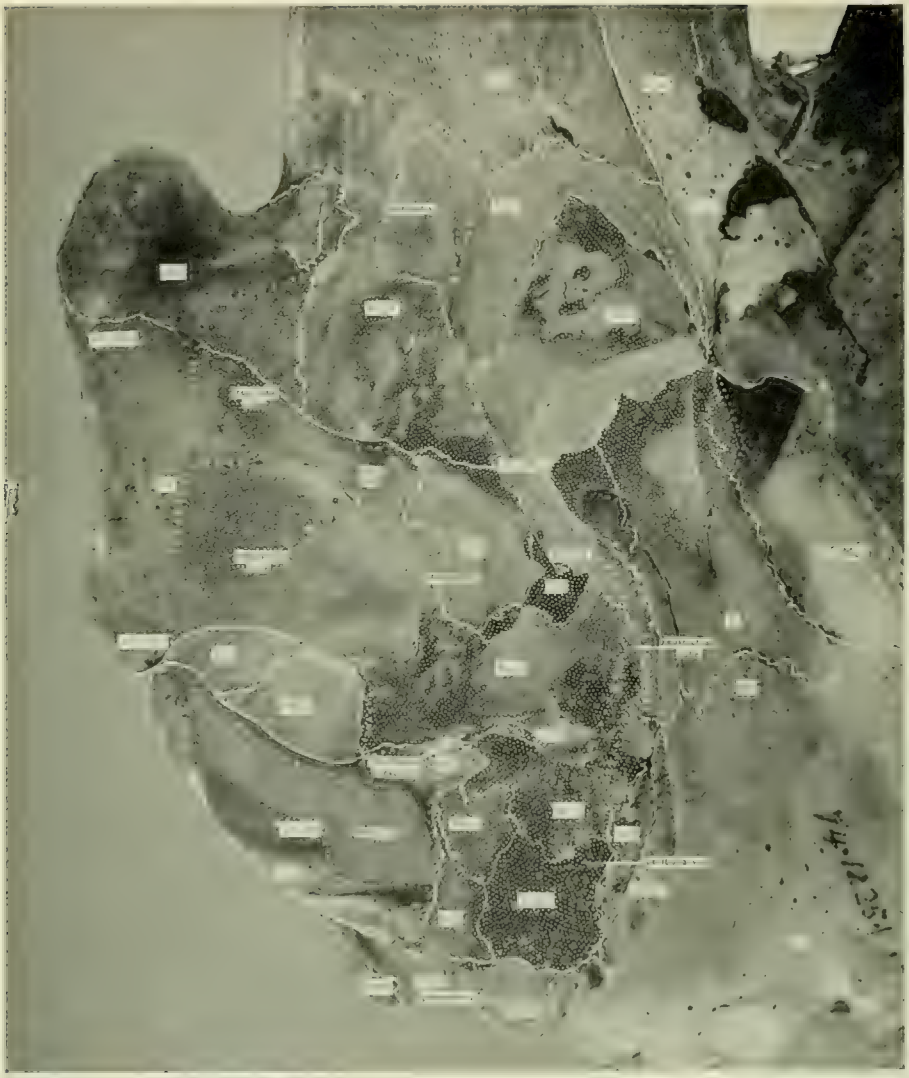


PLATE 35

Feresa intermedia (Reg. No. 1874.11.25.1)

Ventro-lateral aspect of skull base.

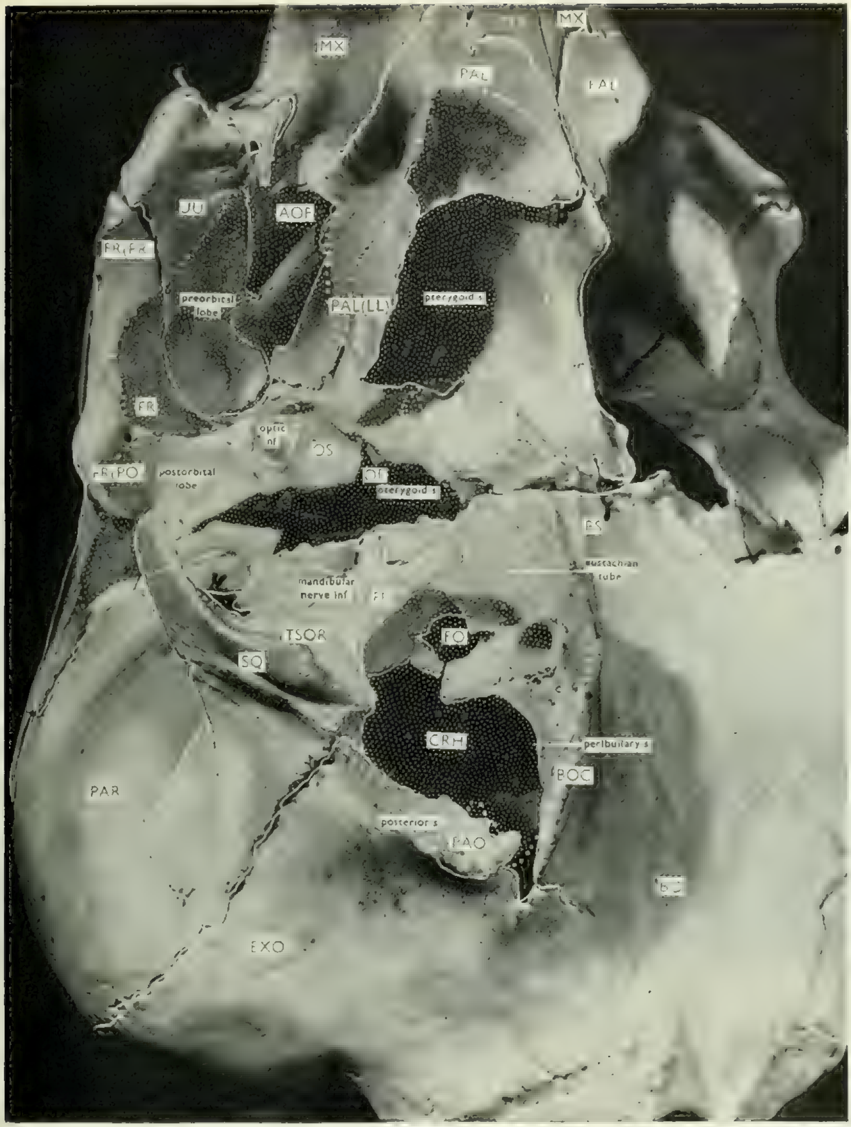

MX
MX
PAL
PAL
JU
AOF
FR,FR
preorbital lobe
PAL(LL)
pterygoid s
FR
optic nf
OS
FR,PO
postorbital lobe
OF
pterygoid s
BS
eustachian tube
mandibular nerve inf
TSOR
SQ
FO
CRH
peribullary s
BOC
PAR
posterior s
PAO
BO
EXO

PLATE 36

Cephalorhynchus heavisidei (Reg. No. 1948.7.27.1)
Ventro-lateral aspect of skull base.

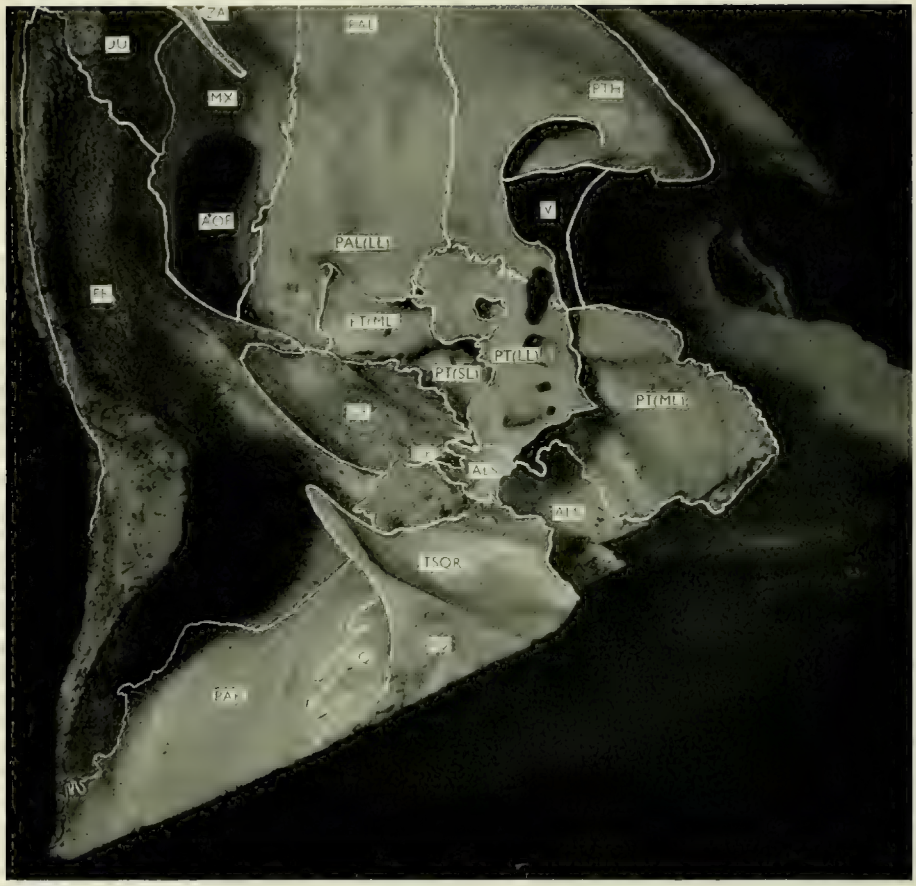

ZA
PAL
JU
MX
PTH
V
AOF
PAL(LL)
FR
PT(ML)
PT(LL)
PT(SL)
PT(ML)
TSQR

PLATE 37

Lagenorhynchus albirostris (Reg. No. S.W.1947/14)
Ventro-lateral aspect of skull base

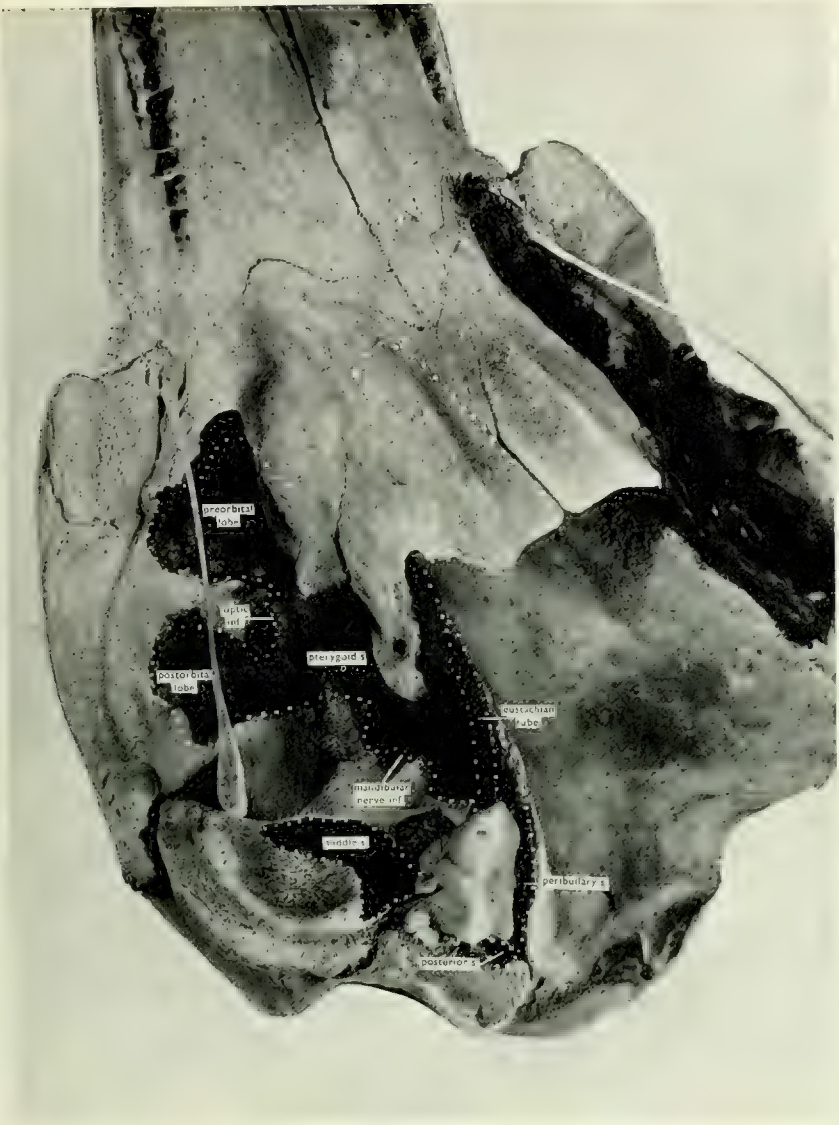

preorbital lobe
optic inf
pterygoid s
postorbital lobe
eustachian tube
mandibular nerve inf
middle s
peribullary s
posterior s

PLATE 38

Lagenorhynchus albirostris (Reg. No. S.W. 1951/9)
Skull showing internal cast of air sinuses.

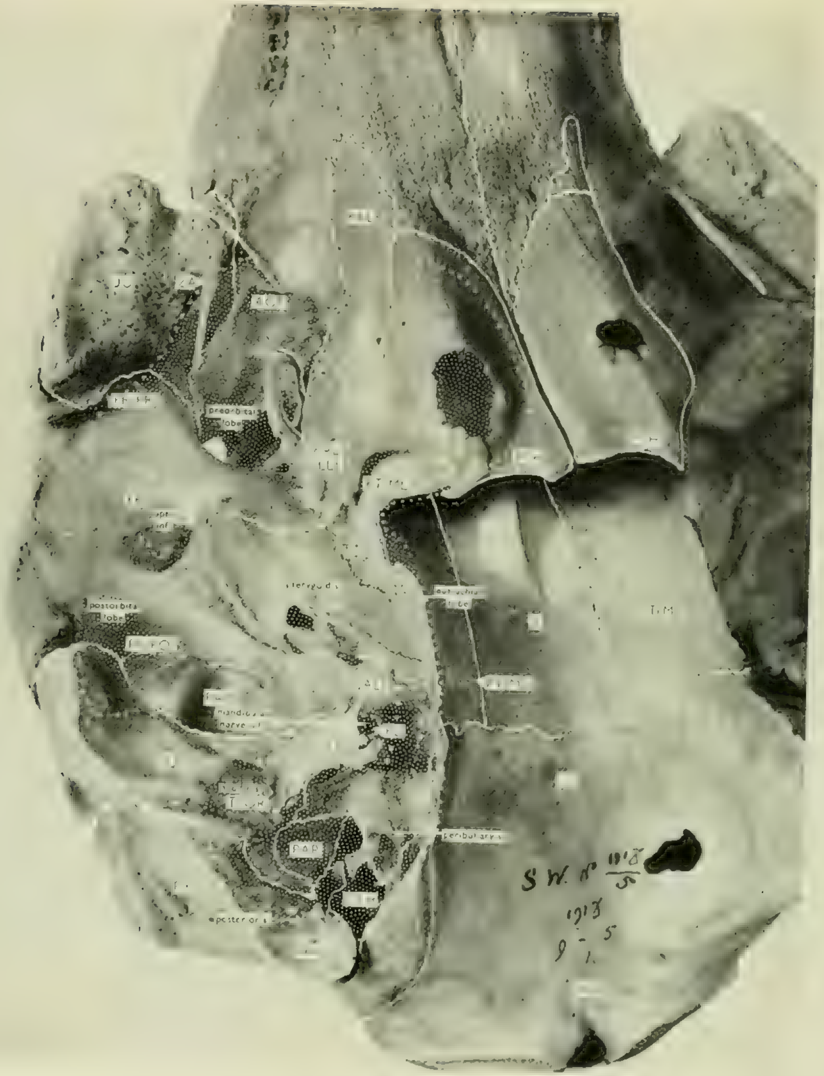

JU
ZA
preorbital lobe
pterygoid s
postorbital lobe
mandibular nerve
PAP
peribullary s
T.M.
S.W. 18 11/8/5
1917
9-5
1.

PLATE 39
Lagenorhynchus acutus (Reg. No. 1917.9.5.1)
Ventro-lateral aspect of skull base.

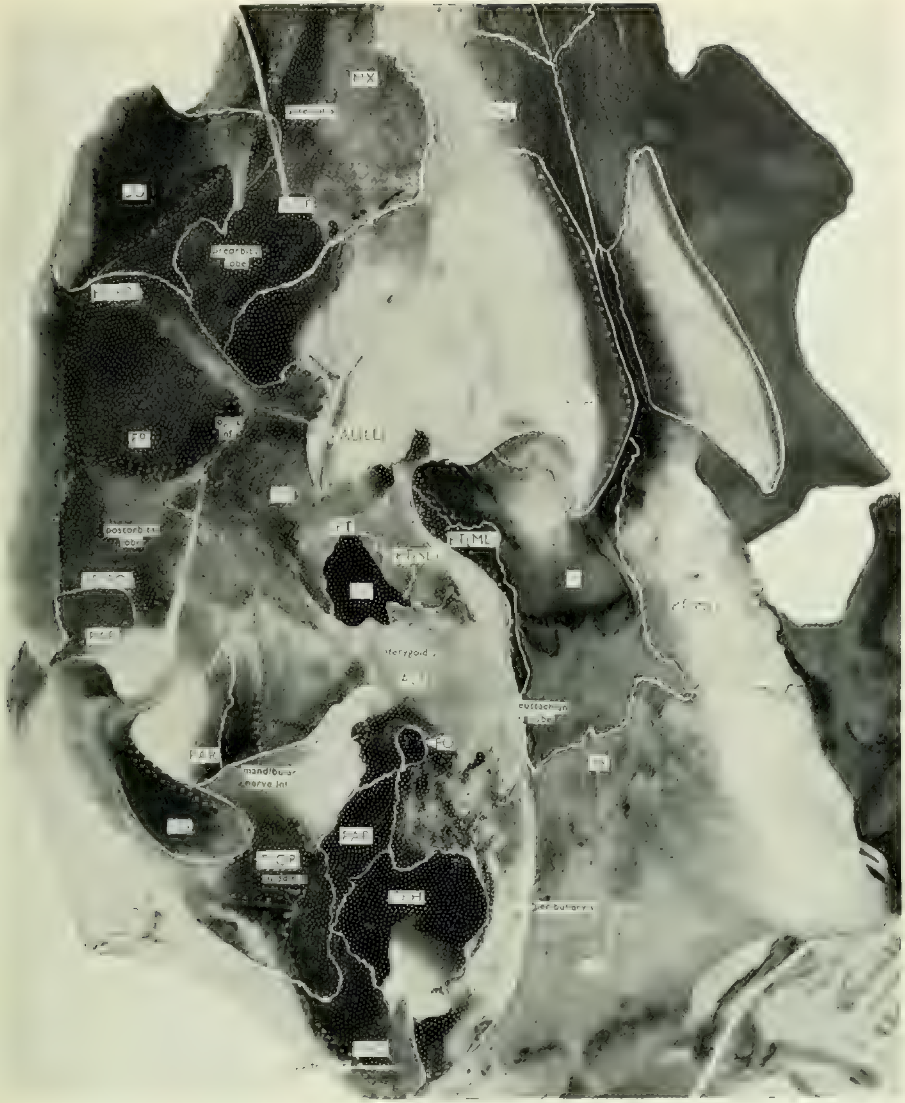

MX
preorbital lobe
FO
postorbital lobe
PT
PTML
PTSL
pterygoid
FAR
mandibular nerve int
FO
FAP
PH
eustachian tube
peribullary

PLATE 40

Lagenorhynchus obscurus (Reg. No. 1944.11.16.1)
Ventro-lateral aspect of skull base.

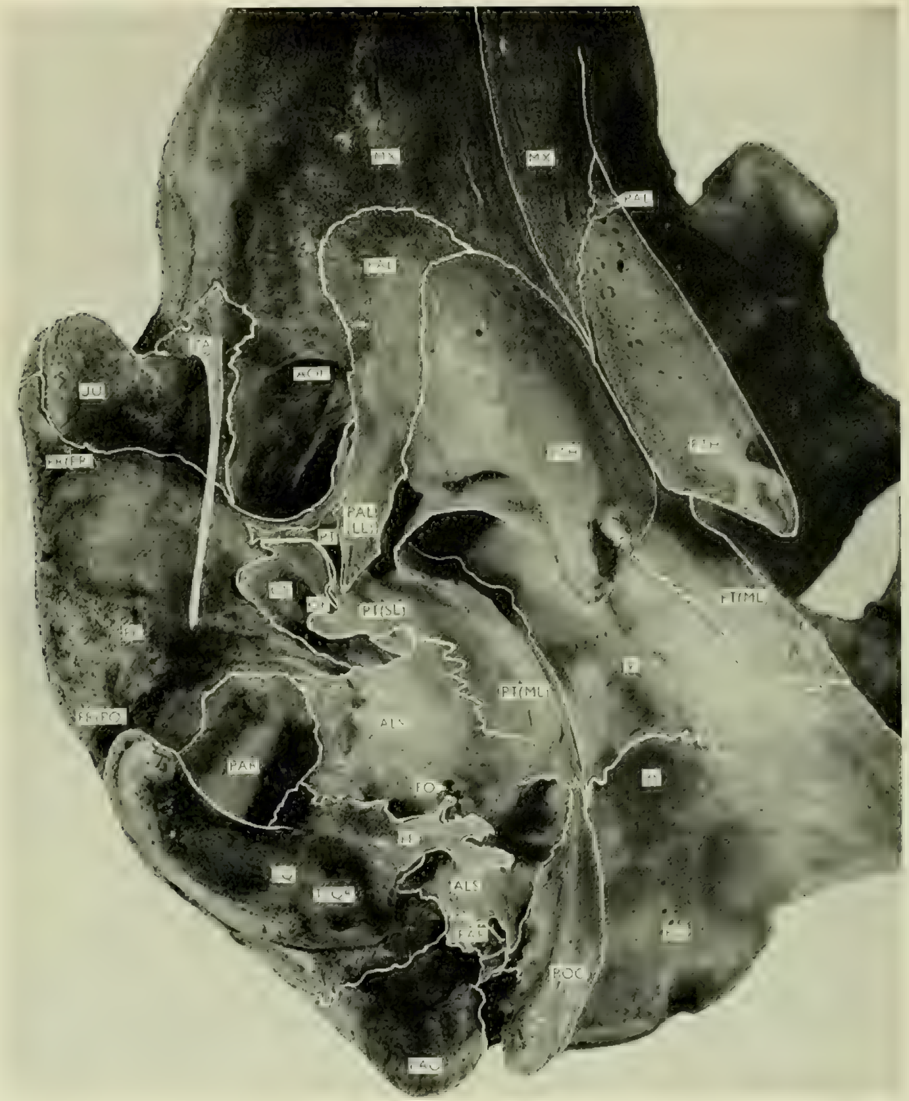

MX
MX
PAL
PAL
TA
JU
FR(FR)
PAL (LL)
PT
PT(SL)
PT(ML)
PT(ML)
FR(PO)
ALS
PAR
FO
ALS
BOC

PLATE 41

Grampus griseus (Reg. No. S.W.1922/7)
Ventro-lateral aspect of skull base.

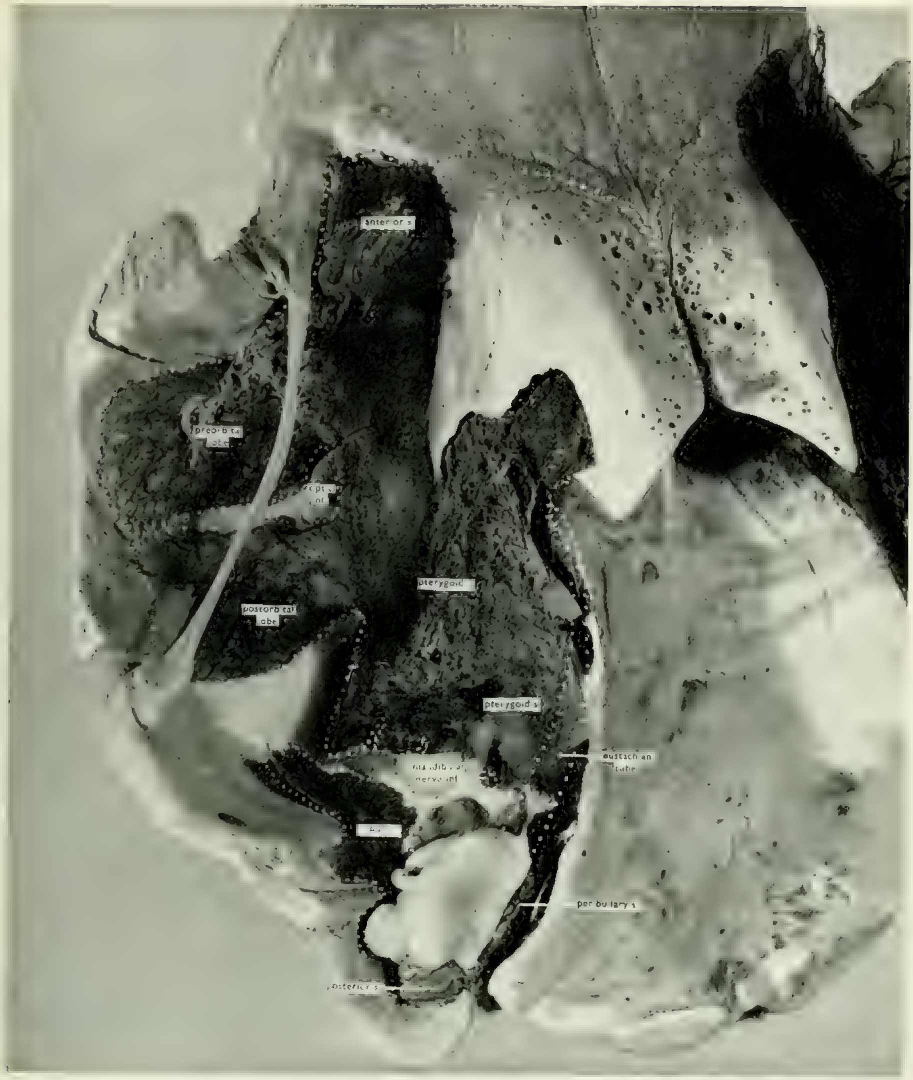

anterior s
preorbital lobe
optic inf
pterygoid
postorbital lobe
pterygoid s
mandibular nerve inf
eustachian tube
peribullary s
posterior s

PLATE 42

Grampus griseus (Reg. No. S.W.1951/3)
Skull showing internal cast of air sinuses.

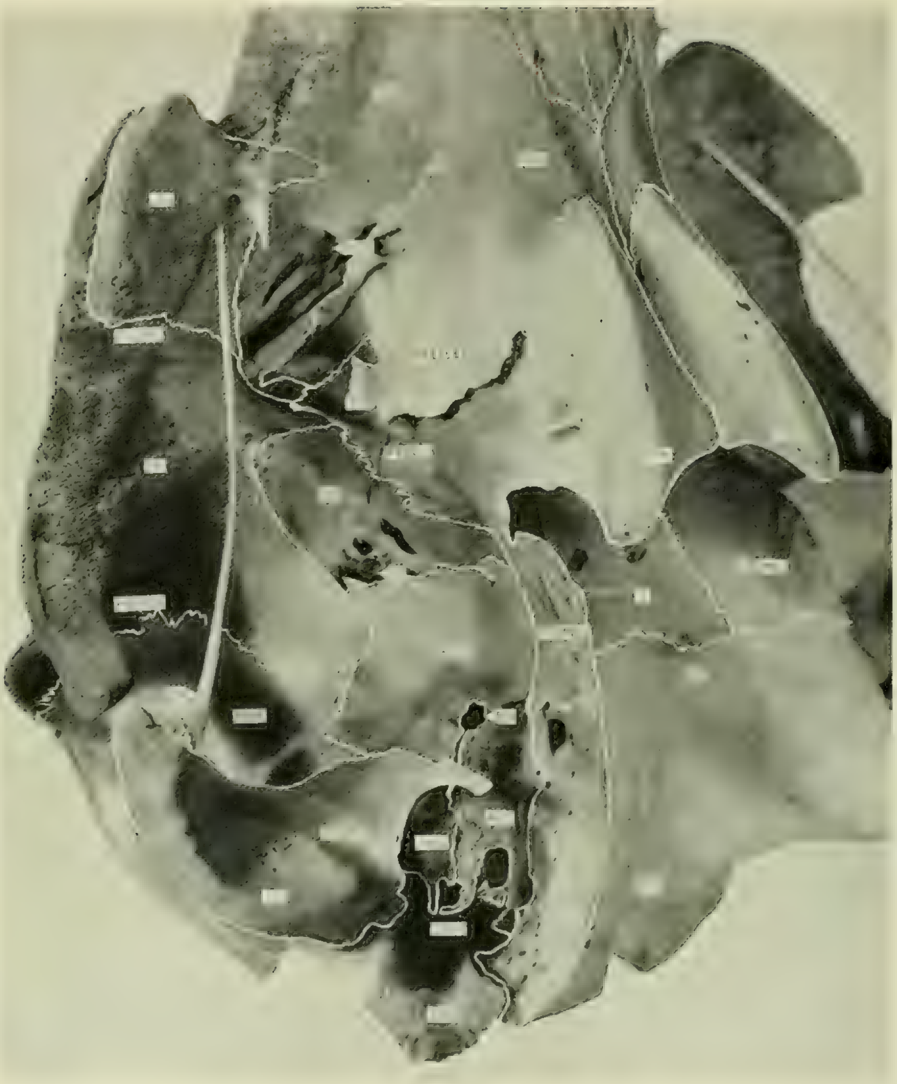


PLATE 43

Tursiops truncatus (Reg. No. 1951.11.26.2)
Ventro-lateral aspect of skull base.

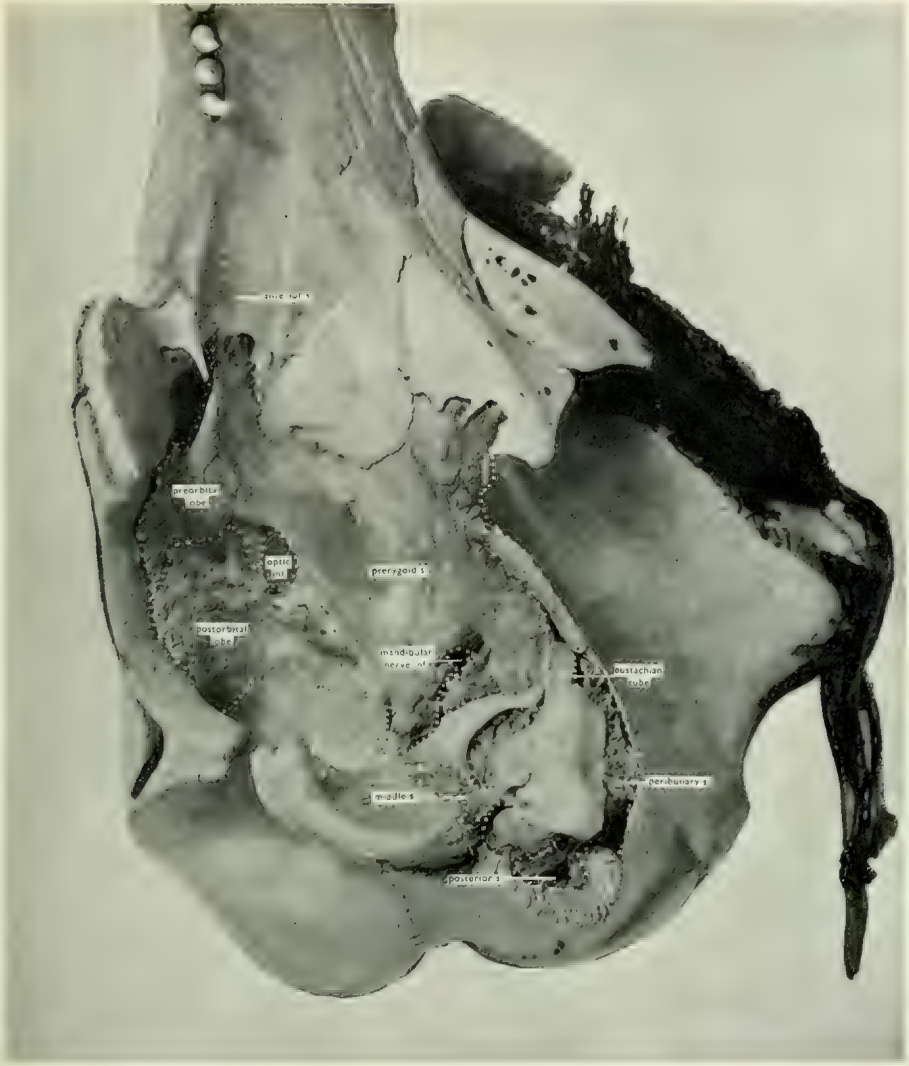

anterior s
preorbital lobe
optic int
pterygoid s
postorbital lobe
mandibular nerve inf
eustachian tube
peribullary s
middle s
posterior s

PLATE 44

Tursiops truncatus (Reg. No. 1951.11.26.1)
Skull showing internal cast of air sinuses.

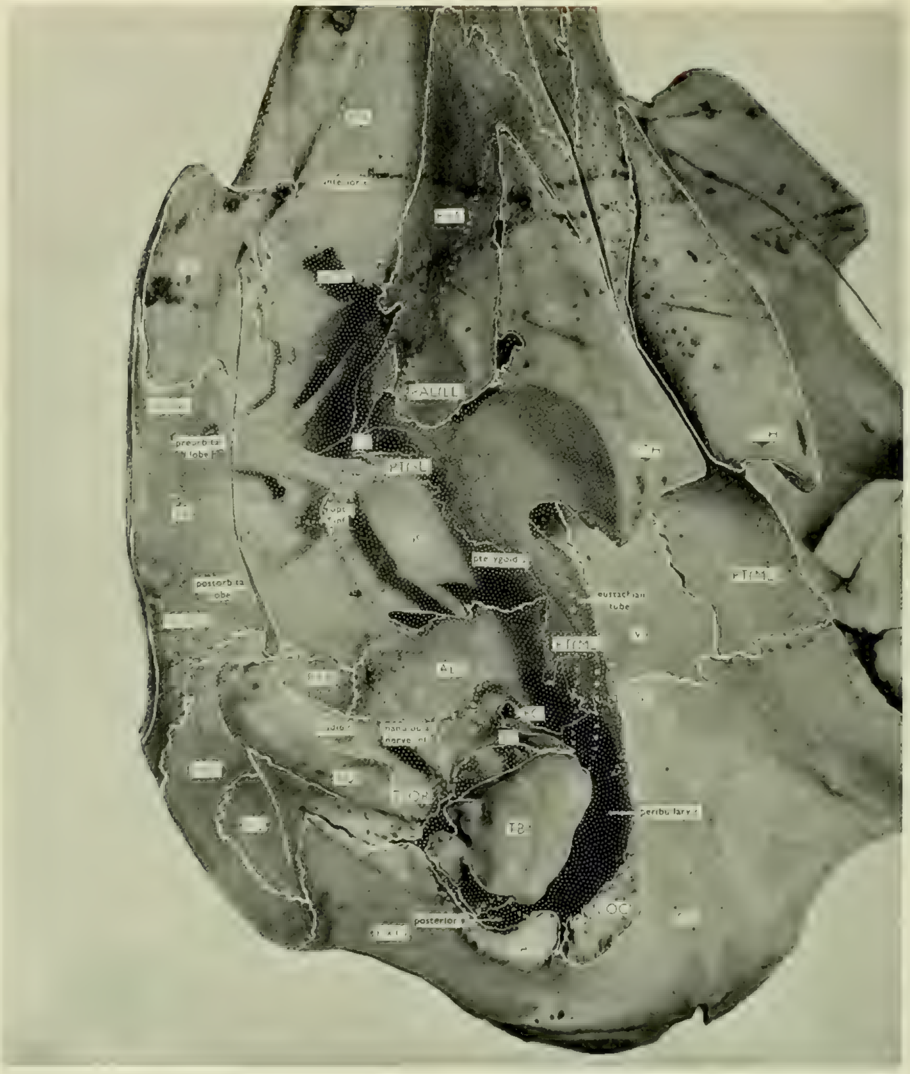

anterior
PAL
preorbital lobe
PTM
opt inf
pterygoid
postorbital lobe
eustachian tube
PTM
AL
mandibular nerve
TB
peribullary
OC
posterior

PLATE 45

Stenella euphrosyne (Reg. No. 1938.2.5.1)

Ventro-lateral aspect of skull base.

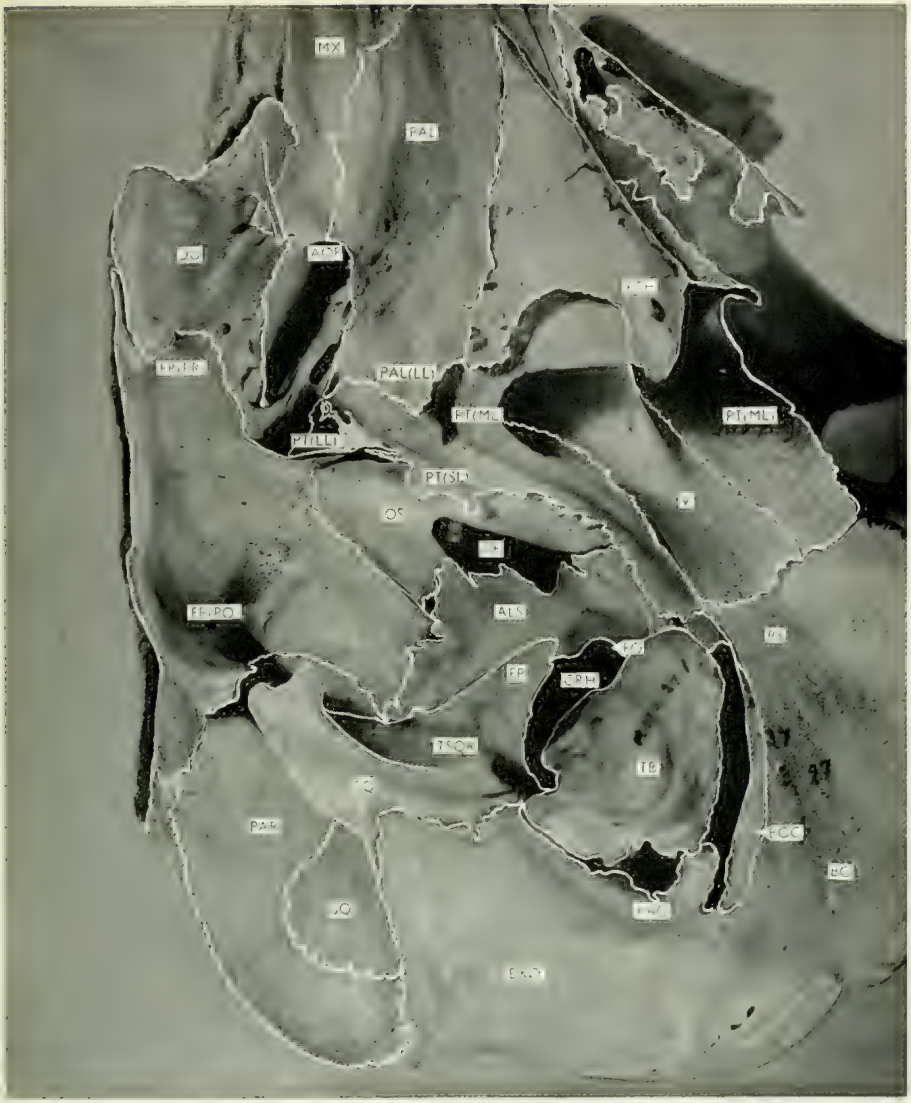

MX
PAL
JU
AOF
PAL(LL)
PT(ML)
PT(ML)
PT(LL)
PT(SL)
OS
V
ALS
FR(PO)
FO
FP
CRH
TSQR
TB
SQ
PAR
SQ
EXO
ECC
BC

PLATE 46

Delphinus delphis (Reg. No. 1937.11.27.1)
Ventro-lateral aspect of skull base.

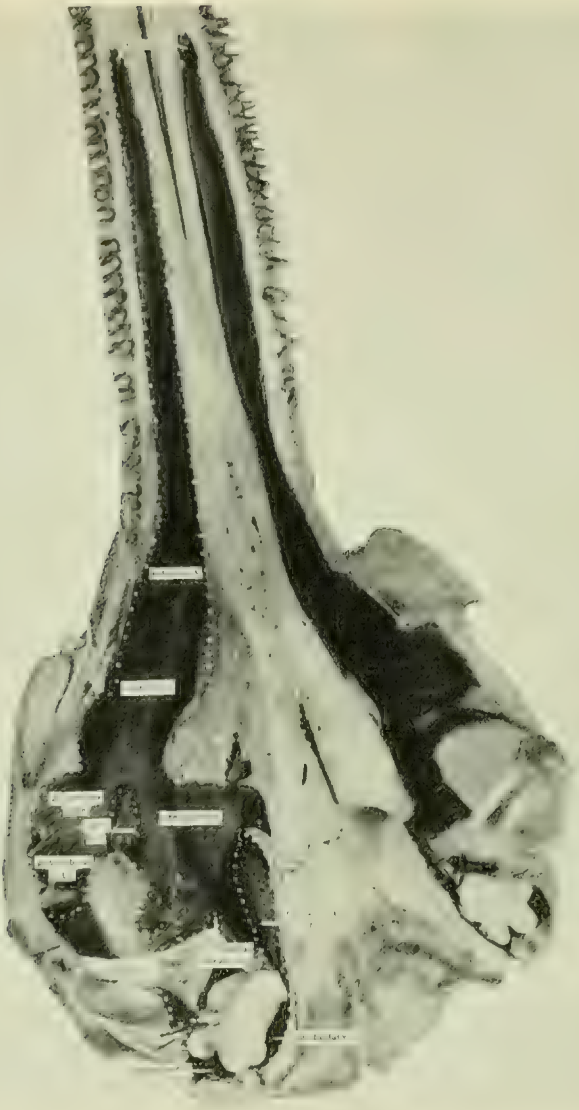


PLATE 47

Delphinus delphis (Reg. No. S.W. 1952/2)
Skull showing internal cast of air sinuses.

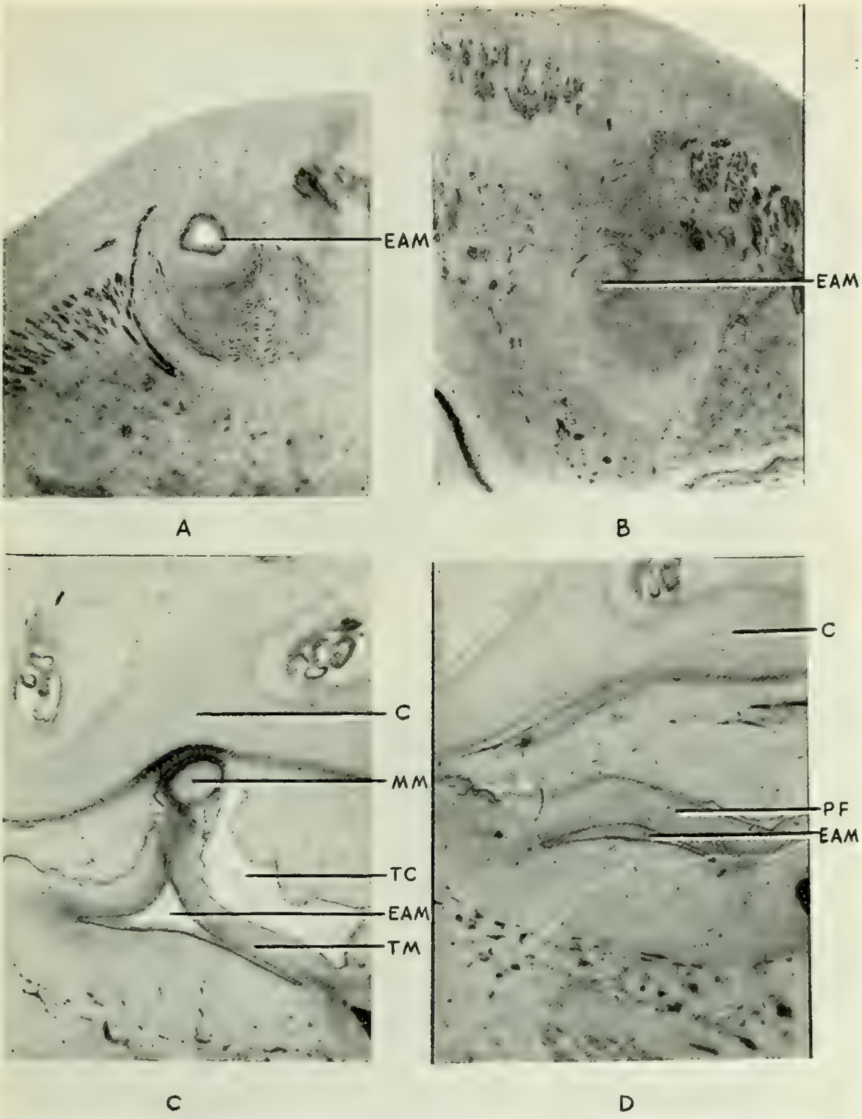


PLATE 48

Longitudinal sections in the region of the ear of a foetal Humpback, *Megaptera novaeangliae*

(A) Distal end of external auditory meatus (× 40).

(B) Closed portion of external auditory meatus (× 40).

(C) Section through tympanic membrane, manubrium mallei and tympanic cavity (× 40).

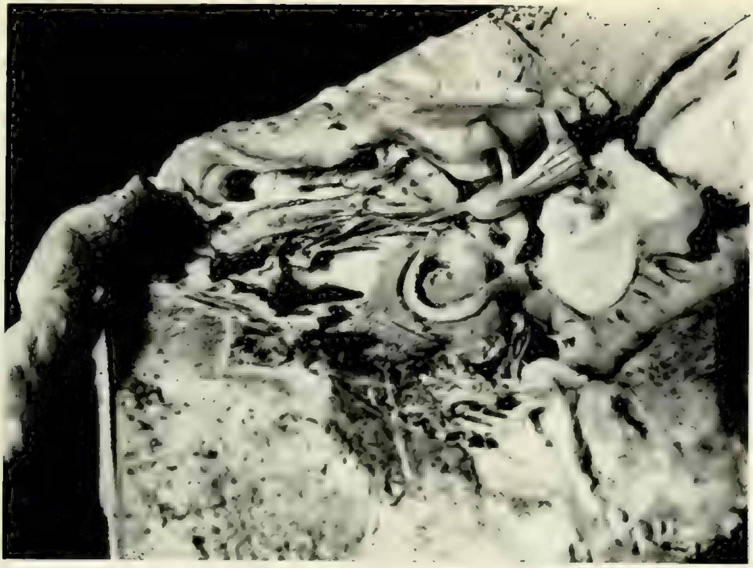
(D) Pars flaccida of the tympanic membrane (× 40).

PLATE 49

Dissection of the middle ear of *Globicephala melaena* (cf. Text-figure 26)

PLATE 50

Dissection of the middle ear of *Balaenoptera acutorostrata* (cf. Text-figure 27)



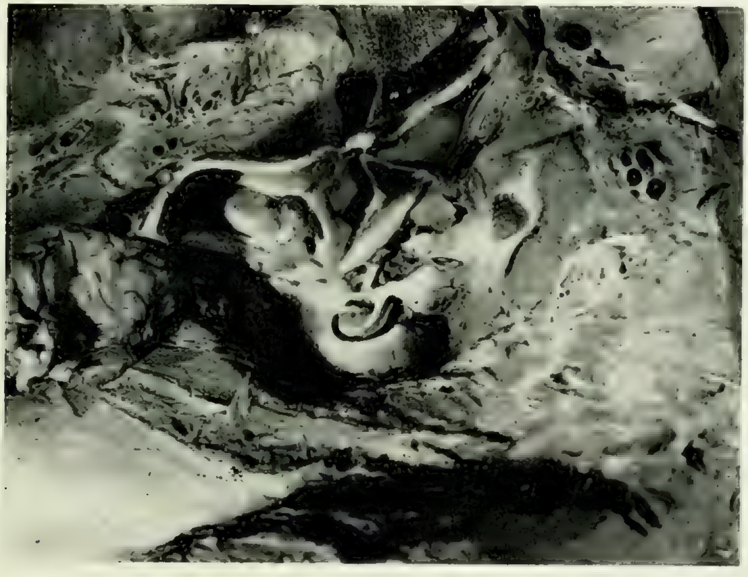


PLATE 51

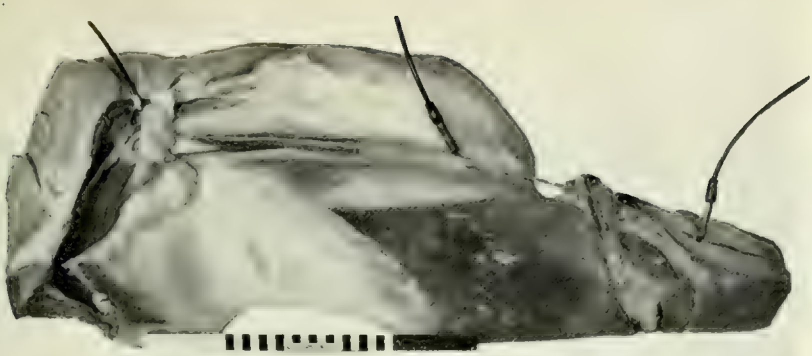
Dissection of the ear of *Balaenoptera physalus*

Starting from the right of the figure the following features in succession open pigmented part of the external meatus with blubber adjacent ; auricular cartilage with muscles attached ; the cord-like portion of meatus, the proximal portion of the meatus lying in the squamo-mastoid groove with part of the corium removed to show the ear plug and glove finger, the tympanic bulla with mesial half removed to show middle ear cavity and pterygoid sinus. Acoustic probes are shown in three of the positions used for testing sound attenuation.

PLATE 52

Dissection of the ear of *Balaenoptera physalus* showing glove finger and ear plug.

The ear plug has been bisected to show laminations, but in life it would completely envelop the glove finger of which it is the zona cornea. The extension of the middle ear cavity into the pterygoid sinus shows part of the fibro-venous plexus (bottom left). Acoustic probes are placed on the malleus and ear plug.



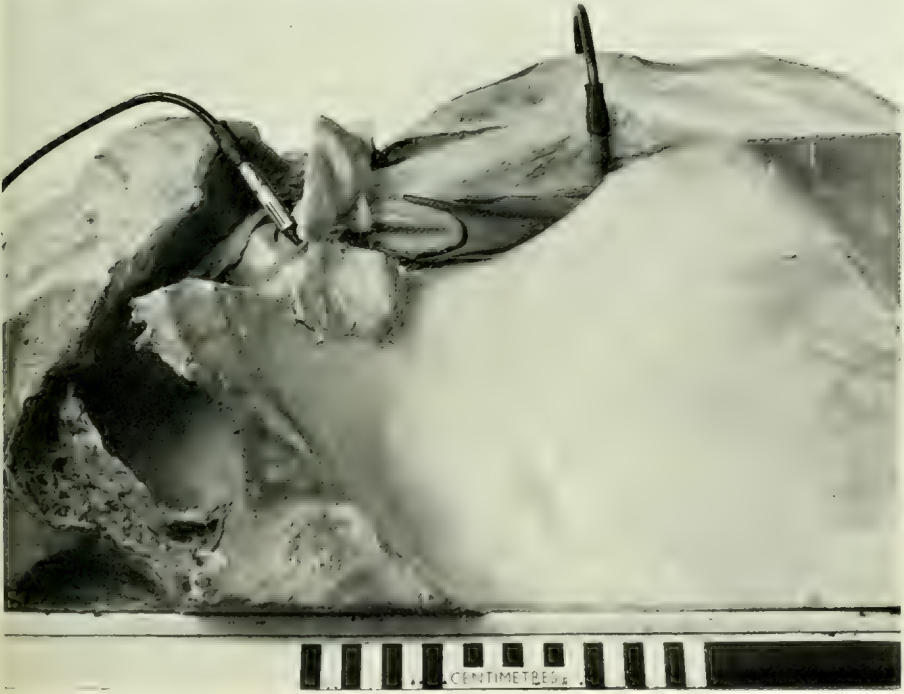
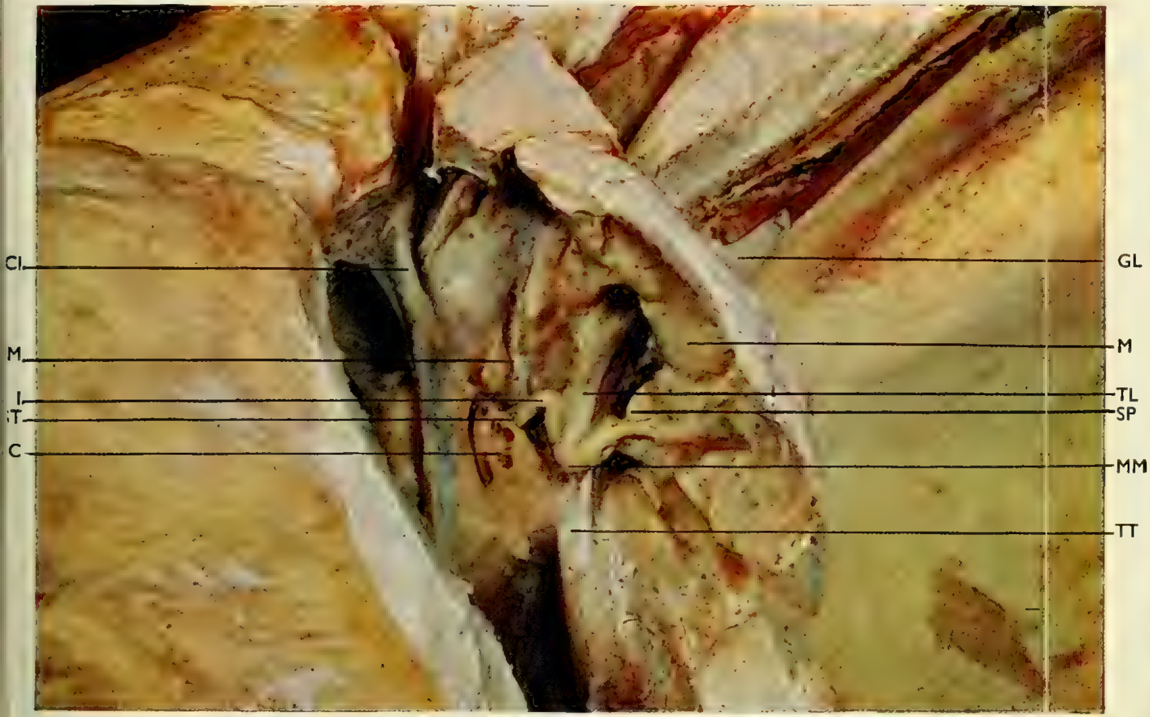

CENTIMETRES

PLATE 53

Dissection of the middle ear and cochlea of *Balaenoptera physalus*

Dissection shows the tympanic ligament (TL) attached to the malleus (MM) which is fused to the sigmoid process of tympanic bulla. The tensor tympani muscle (TT) passes obliquely downwards to the right of the exposed cochlea (C). The incus (I) and stapes (ST) are situated above the cochlea. The atrophied internal carotid artery (ACI) passes obliquely across the tympanic cavity to the left of the cochlea. The groove in which the stapedial muscle (SM) lies can be seen above the cochlea. Note the muscle mass (M) the tendon of which passes through the tympanic annulus to the internal face of the " glove-finger " (Shrapnell's membrane, GL).

By courtesy of " ENDEAVOUR ".


CI
M
I
T
C
GL
M
TL
SP
MM
TT

[illegible]

LES TYPES D'HARPAGOPHORIDAE DE R. I. POCOCK CONSERVÉS AU BRITISH MUSEUM (NATURAL HISTORY) (MYRIAPODES, DIPLOPODES)

14 NOV 1960
PRESENTED

J. M. DEMANGE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 7 No. 2
LONDON : 1960

LES TYPES D'HARPAGOPHORIDAE DE R. I. POCOCK CONSERVÉS AU BRITISH MUSEUM (NATURAL HISTORY) (MYRIAPODES, DIPLOPODES)

1960
SENTED

PAR

J. M. DEMANGE

Laboratoire de Zoologie du Muséum National de Paris

Pp. 141–179 ; 87 *Text-figures*

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THE BRITISH MUSEUM (NATURAL HISTORY)
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NTED

LES TYPES D'HARPAGOPHORIDAE DE R. I. POCOCK CONSERVÉS AU BRITISH MUSEUM (NATURAL HISTORY) (MYRIAPODES, DIPLOPODES)

Par J. M. DEMANGE

AYANT entrepris la révision de la famille des Harpagophoridae nous nous sommes rapidement aperçu qu'une étude particulière devait être consacrée aux espèces décrites par les Auteurs il y a une cinquantaine d'années.

La plupart des descriptions sont en effet succinctes, souvent imprécises et non illustrées. De plus les figures publiées à l'époque sont petites et ne montrent qu'une partie des gonopodes. De ce fait beaucoup de ces espèces ne peuvent être identifiées et figurent dans une trop longue liste de " Species incertae sedis ".

C'est pour cette raison que nous nous sommes rendu à Londres pour étudier les types de R. I. POCOCK conservés au British Museum.

Le Dr. G. O. EVANS, directeur de la section des Arachnides, nous a ouvert largement ses collections et ses laboratoires où nous avons trouvé de la part de MM. E. BROWNING, K. H. HYATT, et D. MACFARLANE une aide précieuse. Nous sommes heureux de trouver ici l'occasion d'exprimer au Dr. G. O. EVANS et à ses collaborateurs toute notre reconnaissance et nos remerciements pour leur sympathique et cordial accueil.

Nous nous proposions d'examiner 32 espèces qui sont les suivantes :

Rhynchoproctus proboscideus
Spirostreptus asthenes
aterrimus
baluensis
bowringii
centrurus
doriae
dulitianus
everettii
exocoeti
feae
gestri
hosei
insculptus
jerdani
moseleyi
Spirostreptus oatesii
patricii
perakensis
regis
stenorhynchus
tavoiensis
Thyropygus andersoni
anurus
aulaconotus
erythropleurus
pachyurus
rubrocinctus
rubrolimbatus
weberi
xanthonotus
xanthurus

Malheureusement 17 seulement ont pu être examinées auxquelles nous avons ajouté *Spirostreptus vittatus* Newp. dont, à notre connaissance, aucune figure précise n'a été publiée.

Des 15 espèces restantes, 6 n'ont pu être retrouvées étant conservées, sans doute, dans un Musée que nous ignorons. Il s'agit de *Thyropygus andersoni*, *perakensis*, *Spirostreptus doriae*, *exocoeti*, *jerdani*, *regis* ; 6 basées sur des ♀ ou ♀ et ♂ juv. : *Thyropygus erythropleurus* (♀ et ♂ juv.), *xanthonotus* (♀), *xanthurus* (♀ *et* ♂ *juv.*), *Spirostreptus asthenes* (♀), *insculptus* (♀), *moseleyi* (♀).

Par contre les 3 espèces suivantes, *Thyropygus aulaconotus*, *pachyurus*, *rubrolimbatus* n'étaient représentées, comme type dans la collection que par le sexe ♀ bien qu'ayant été décrites sur les deux sexes à l'exception de *rubrolimbatus* basé sur un unique ♂ (coquille d'imprimerie probablement puisqu'il n'est fait mention dans la description d'aucun organe copulateur, ni de caractères sexuels secondaires). Nous avouons ne pas bien comprendre ce qui a pu se passer pour les deux premières espèces. Nous supposons que la ♀ seule a été prise comme " type ", le ♂ comme " cotype ", celui-ci ayant été envoyé par l'Auteur à l'un de ses collègues. Nous précisons à ce sujet que H. W. Brölemann possèdait dans sa collection personnelle, maintenant conservée au Muséum National d'Histoire Naturelle de Paris, un certain nombre de types et " cotypes " dont un *Spirostreptus feae* sur lequel nous reviendrons.

Quoiqu'il en soit nous ne pouvons actuellement faire état de ces espèces dans notre systématique.

Ajoutons enfin que seul le " cotype " de *Thyropygus anurus* a été retrouvé et que 5 bocaux renfermaient des specimens n'étant pas désignés comme type. Il s'agit de *Spirostreptus aterrimus*, *dulitianus*, *oatesii*, *tavoiensis* et *Thyropygus gestri*. Nous considèrons les individus comme types et ce pour les raisons que nous exposons au cours de leur description.

L'étude des types de R. I. Pocock pose naturellement certains problèmes de systématique et de synonymie que nous ne voulons pas résoudre ici nous réservant d'envisager ces problèmes dans un travail plus complet, en cours de rédaction, constituant les premiers éléments d'une révision de la famille.

DESCRIPTION DES ESPÈCES EXAMINÉES

Les descriptions qui vont suivre concernent plus particulièrement les gonopodes mais nous avons adjoint quelques renseignements morphologiques généraux comme les sillons collaires, la forme de la cavité stigmatique, les soles etc.

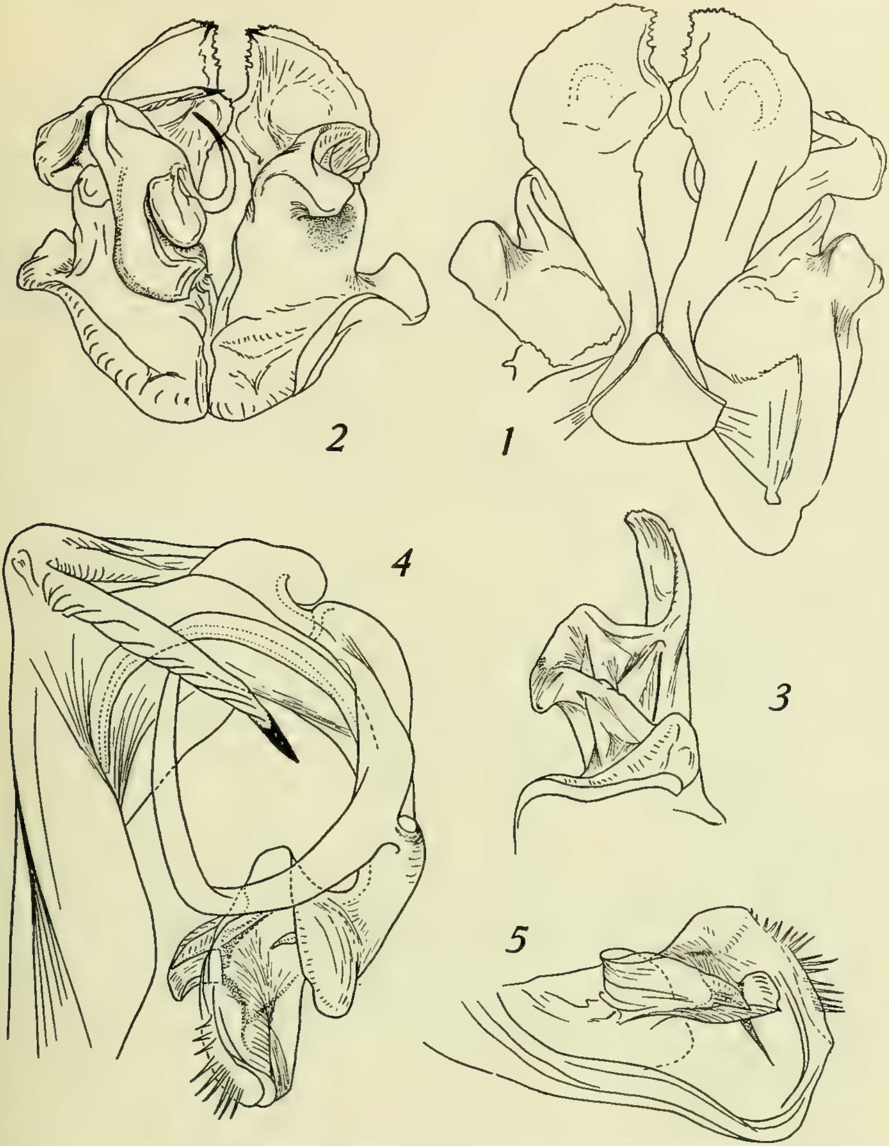
Chaque nom d'espèce est suivi de la station de récolte et d'une série de numéros correspondant à la référence du British Museum.

Spirostreptus bowringii Pocock, 1892 " Type "

Journ. Lin. Soc. **24** : 321.

Siam. Bowring. Reg. No. 1960.2.2.1.

♂. 59 segments.



FIGS. 1–5. *Spirostreptus bowringii* Poc. Fig. 1. Gonopodes, face antérieure. Fig. 2. Gonopodes, face postérieure. Fig. 3. Hanche, profil externe. Fig. 4. Télopodite. Fig. 5. Extrémité du télopodite.

Collum à lobe en angle droit, étroit, à bourrelet à peu près régulier. 4 à 5 plis sur la surface y compris quelques griffures au bord postérieur.

Sternite du dernier segment entièrement libre.

Cavité stigmatique allongée.

Soles sur les deux avant-derniers articles de la 3ème paire à la dernière.

Gonopodes à sternite triangulaire de grande surface, à angles arrondis.

Feuillet coxal postérieur (fig. 1) étroit à la base puis brusquement élargi par un épanouissement en palette incliné vers l'intérieur. Bord externe, d'abord droit en partant de la base, s'inclinant fortement vers l'intérieur et portant, à la partie supérieure, un grand nombre de petites dents aiguës. Lobe interne échancré en demi-cercle sur son bord dessinant ainsi une large denticulation et un angle robuste dirigé distalement, à bord finement dentelé. Le lobe dentiforme se superpose à son homologue en se croisant.

Feuillet coxal antérieur débutant, en avant, par une large pièce dont l'angle externe est souligné par une forte protubérance arrondie et élevée. Bord latéral du feuillet, constituant les lèvres de l'orifice de la gaine coxale, se retournant vers l'arrière, en s'épaississant, face postérieure, en un large bourrelet arrondi, recourbé vers la base de l'organe puis s'amincissant en épaisse lamelle latérale interne qui s'incline vers l'orifice de la gaine coxale en une sorte de tablier horizontal avant de rencontrer le feuillet précédent (figs. 2 et 3).

Télopodite (figs. 4 et 5) court et épais. Branche montante épaissie, à sa sortie de la gaine coxale, par un bourrelet horizontal, en forme de haricot, de l'avant duquel jaillit une très longue épine fémorale courbée vers l'arrière dans le même plan que l'épaississement et pourvue de plis hélicoidaux à la face inférieure. Télopodite étranglé après l'angle postérieur du bourrelet qui est en quelque sorte la limite du fémur et recourbé vers la base de l'organe puis brusquement épanoui en lame complexe à partir d'un puissant talon. Arête interne, dans le sens de la courbure, projetant une très longue épine tibiale grêle recourbée en arc de cercle et remontant vers la grande courbure.

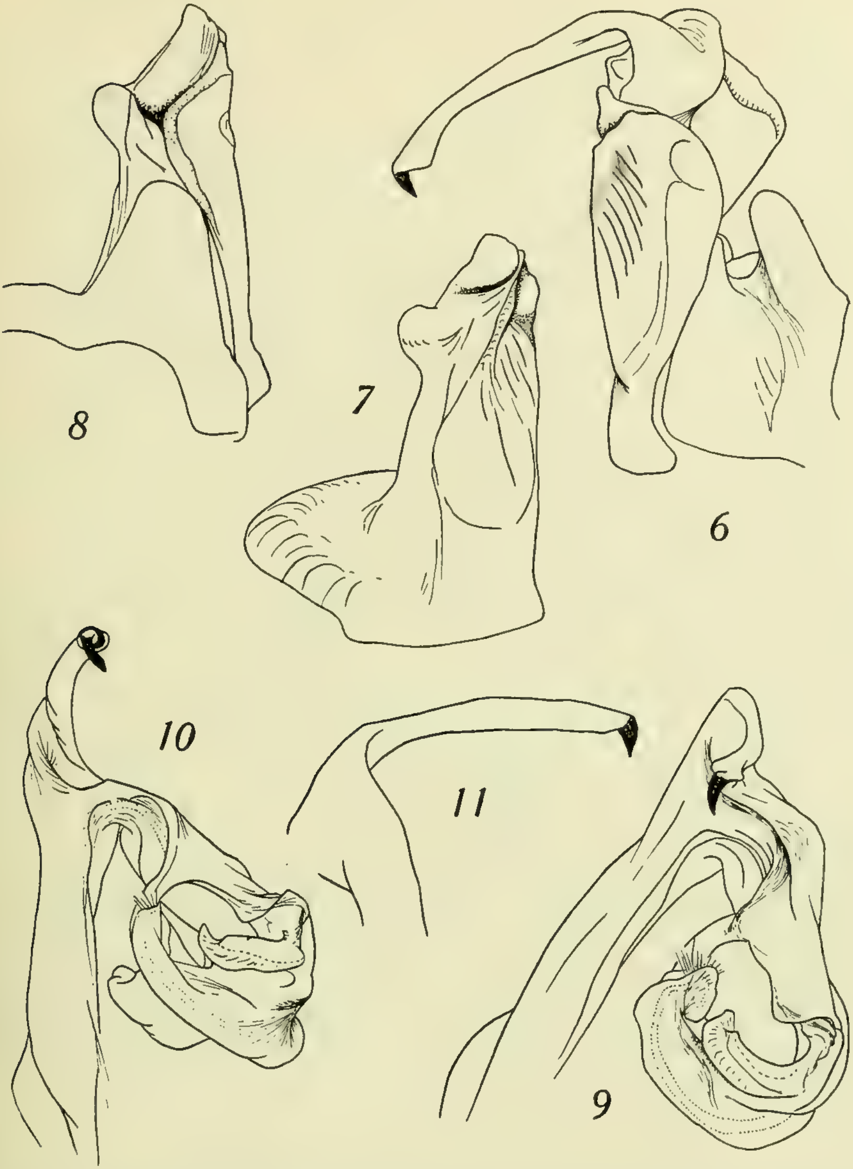
Extrémité distale du membre (fig. 5) élargie en plage arrondie portant, à son extrémité, l'orifice du canal séminal entouré d'une dizaine d'épines de grosseurs progressives. Bord lamellaire de cette plage retourné sur lui-même, sinueux, en forme de S donnant naissance à une petite plage moyenne située au-dessus de l'épanouissement distal, sous l'épine tibiale et dessinant, avec elle, une large gouttière par son mouvement hélicoidal. Axe longitudinal de la face inférieure de la plage distale principale soulevé en une lamelle hyaline à bords sinueux et plus ou moins rabattue à laquelle se rattache une deuxième formation transversale, plus courte que la précédente, reliant celle-ci au bord latéral de la gouttière.

Spirostreptus aterrimus Pocock, 1889 " Type "

Journ. Lin. Soc. **21** : 295.

Mergui. Dr. Anderson. Reg. No. 1889.4.24.13.

Aucun type n'était désigné. L'exemplaire examiné étant le seul ♂ de la station type et le seul disséqué par Pocock nous le considérons comme tel.



Figs. 6–11. *Spirostreptus aterrimus* Poc. Fig. 6. Gonopode gauche, face antérieure. Fig. 7. Hanche du gonopode gauche, profil interne. Fig. 8. Hanche droite, profil externe. Fig. 9. Télopodite. Fig. 10. Télopodite. Fig. 11. Epine fémorale.

♂. 67 segments.

Collum à lobe en angle obtus. Bourrelet marginal fort. Pas de sillons sur la surface.

Sternite du dernier segment soudé.

Cavité stigmatique en triangle allongé.

Soles de la 3ème paire de pattes à la dernière sur les deux avant-derniers articles. Seule la 3ème paire de pattes porte des soles sur l'avant-dernier article.

GONOPODES abimés par l'Auteur. Les deux hanches sont séparées l'une de l'autre et nous n'avons pu retrouver le sternite, bien que la trace semble demeurer.

Feuillet coxal postérieur (fig. 6) très étroit à la base et rapidement élargi en palette vers l'extrémité. Sommet arrondi plus particulièrement à la partie latérale externe. Portion latérale interne rapidement élevée en angle aigu. Bord latéral interne du sommet fortement relevé en crête tranchante particulièrement soulignée, face latérale interne, par un sillon très profond (fig. 7) se perdant dans le milieu de la hanche. A cette même face interne se détache près du sommet un lobe épais et arrondi.

Feuillet coxal antérieur élevé et latéralement armé d'une haute et importante protubérance conique.

Télopodite (figs. 9, 10 et 12) très volumineux, presque aussi volumineux que les hanches, débouchant au sommet de la gaine coxale.

Dès sa sortie de la gaine coxale la branche montante s'épaissit, devient légèrement globuleuse, se coude en angle droit et s'étale en feuillet recroquevillé en nombreux plis dans le sens longitudinal et enroulé sur lui-même en un cercle presque complet. A partir de la grande courbure, dans la concavité, se différencie un fort épaississement élevé conduisant la rainure séminale et allant en diminuant de volume jusqu'à disparaître près de l'extrémité. Bord latéral interne replié et épanoui en lobe subrectangulaire portant une longue et épaisse épine tibiale dont la pointe se dirige vers l'extrémité du membre, creusée en gouttière.

On remarque que le bord latéral externe poursuit sa course jusqu'aux épines distales mais que le bord latéral interne amorce un mouvement hélicoidal tout en poussant un important processus qui devient globuleux à l'extrémité et dont le plan est perpendiculaire à l'extrémité du membre portant les épines tout en s'enroulant autour de lui. Il se forme ainsi une gouttière hélicoidale s'enroulant autour de l'axe du membre et dont l'un des bords (correspondant au bord latéral interne) est considérablement aminci en feuillet hyalin.

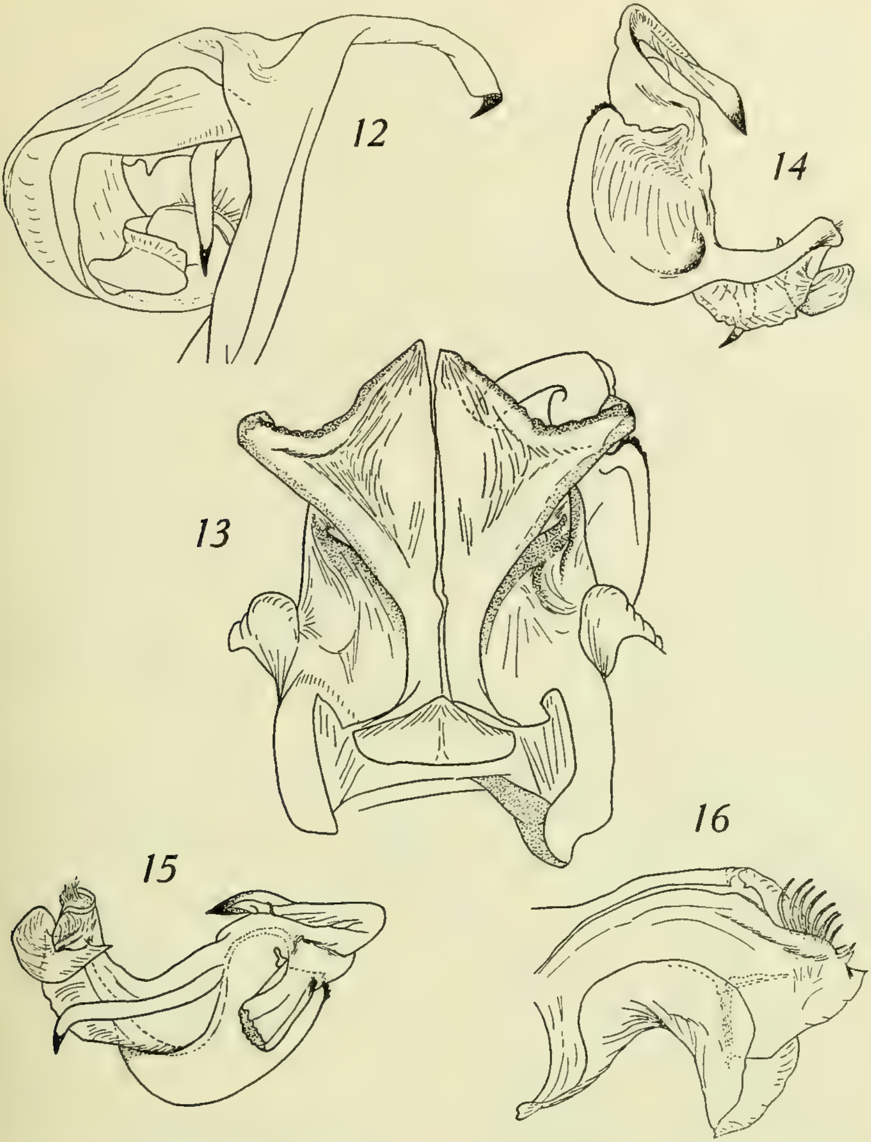
Grande courbure du télopodite surmontée d'une épine particulièrement développée, pliée à sa base en angle droit et se dirigeant face latérale interne. Pointe de cette épine très aplatie et pliée sur elle-même (fig. 11).

Thyropygus weberi Pocock, 1894 " Type "

Max Weber—Zool. Ergeb. III : 382.

Alahang Pandjang. Reg. No. 1896.10.6.76.

♂. 67 segments.



Figs. 12–16. *Spirostreptus aterrimus* Poc. Fig. 12. Télopodite. *Thyropygus weberi* Poc. Fig. 13. Gonopodes, face antérieure. Fig. 14. Télopodite de profil. Fig. 15. Télopodite. Fig. 16. Extrémité distale du télopodite.

Collum à angle antérieur du lobe saillant légèrement. Bourrelet marginal normal. 1 à 2 rides sur la surface et quelques griffures près du bord postérieur.

Sternite du dernier segment complètement soudé.

Cavité stigmatique très allongée latéralement.

Soles sur les deux avant-derniers articles de la 3ème paire de pattes à la dernière. Seule la 3ème paire de pattes porte une sole sur l'avant-dernier article.

Gonopodes à sternite triangulaire avec une large dépression verticale médiane. Sillons de la surface profonds.

Feuillet coxal postérieur (fig. 13) étroit à la base s'évasant brusquement en palette triangulaire large. Bord interne droit. Bord externe largement prolongé par un processus très développé latéralement. Sommet en pointe aiguë. Surface antérieure finement et profondément striée particulièrement dans les angles.

Feuillet coxal antérieur muni d'une gorge délimitant un bourrelet conique.

Télopodite (figs. 14 et 15) large et spiralé à base pourvue, à sa sortie du fourreau coxal, d'une grosse épine fémorale longue et épaisse, à pointe avec talon proximal, cannelée face inférieure. Epine recourbée en demi-cercle vers l'intérieur.

Le membre est complètement recourbé vers le bas à partir de l'épine fémorale, tout en s'élargissant et s'amincissant en plage pour se terminer en une mince feuille dont le bord latéral s'enroule pour former une large gouttière tout en se recourbant à nouveau en fer à cheval. Extrémité distale du bord de ce feuillet se continuant sous l'extrémité du membre, passant sur la face opposée de cette extrémité pour se souder à elle. Examinée de face (fig. 15) cette portion complexe a la forme générale d'une gouttière, constituée par le bord lamellaire hyalin, dans laquelle se couche l'extrémité proprement dite du télopodite qui est elle-même lamellaire à l'exception du bord épaissi qui conduit la rainure séminale et de son embouchure entourée des épines classiques (fig. 16).

Portion moyenne du télopodite (fig. 14), sous la grande courbure, fortement différenciée en lame épaisse, subrectangulaire face postérieure, à angle antérieur arrondi, fortement saillant vers l'arrière et denticulé. Portion inférieure concave enroulée en cornet. Sur la face opposée est plantée une large et longue épine tibiale en angle droit, de même direction que le membre.

Le télopodite présente de nombreuses sinuosités et mouvements de torsion qui lui donnent un aspect tourmenté.

Thyropygus rubrocinctus Pocock, 1894 " Type "

Max Weber—Zool. Ergeb. III : 382.

Paningaham. Reg. No. 1896.10.6.75.

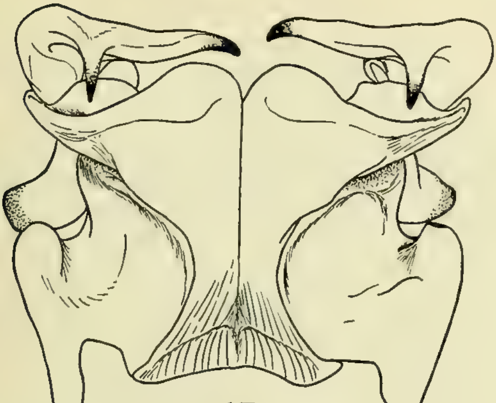
♂. 66 segments.

Collum avec un large bourrelet marginal. Pas de sillons sur la surface.

Sternite du segment terminal entièrement soudé. Valves (fig. 22).

Soles sur les deux avant-derniers articles de la 3ème paire de pattes à la dernière (les 2 dernières paires de pattes sont absentes). 3ème paire de pattes avec sole seulement sur l'avant-dernier article.

Pores répugnatoires débutant sur le 6ème segment.



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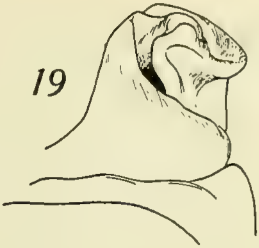

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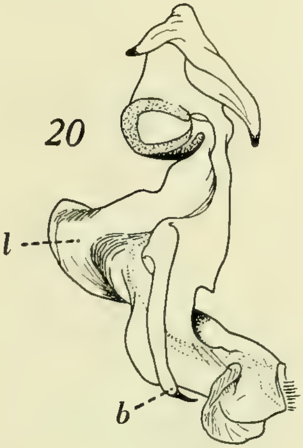

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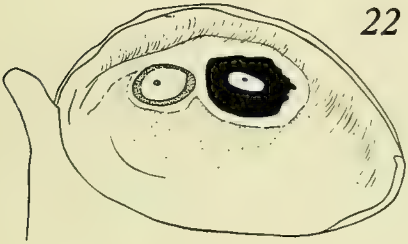

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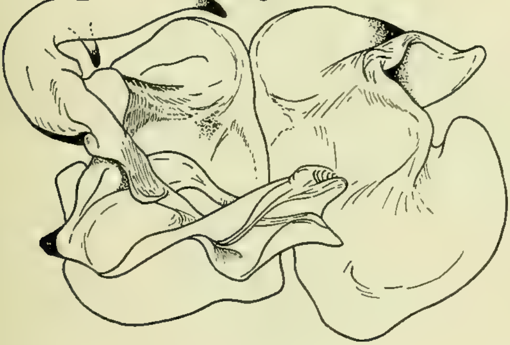

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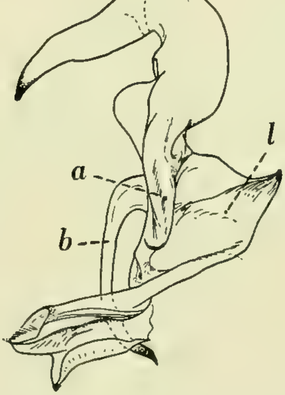

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Figs. 17–22. *Thyropygus rubrocinctus* Poc. Fig. 17. Gonopodes, face antérieure. Fig. 18. Gonopodes, face postérieure. Fig. 19. Hanche gauche, profil externe. Fig. 20. Télopodite. Fig. 21. Télopodite. Fig. 22. Extrémité postérieure du corps. *a.* épaississement du télopodite, *b.* épine tibiale, *l.* lobe du télopodite.

Gonopodes à sternite complètement soudé à la base des feuillets coxaux et portant des traces de division sous forme d'un sillon vertical profond. Le sternite n'est indiqué en quelque sorte que par un relief un peu plus accusé et une couleur différente. Cette région proximale est finement striée longitudinalement.

Feuillet coxal postérieur (fig. 17) étroit jusque près de la moitié puis brusquement épanoui latéralement en une large palette triangulaire. Les angles latéraux externes sont particulièrement développés et allongés. Sommet sinueux et arrondi. La partie supérieure du feuillet est entièrement épaissie face postérieure et forme une sorte de plateforme en cuvette (fig. 18) qui se raccorde d'une part à l'angle externe de la palette et d'autre part au feuillet suivant. Orifice de la gaine coxale (figs. 18 et 19) arrondi, à lèvres fortement saillantes en arrière et latéralement tout en se redressant vers le haut. Cet orifice, juste suffisant pour laisser passer le télopodite, est en quelque sorte constitué par les feuillets coxaux enroulés en cornet et c'est l'angle externe du feuillet postérieur qui fait largement saillie.

Feuillet coxal antérieur (fig. 18), face antérieure, volumineux et large, presque aussi haut que le précédent et creusé au sommet d'une profonde rigole déterminant une saillie conique latérale.

Télopodite très complexe et volumineux (figs. 20 et 21). Dès sa sortie de la gaine coxale, où il est à peine libre, il se recourbe en angle droit s'épaississant considérablement tout en poussant, vers le haut, une très importante épine recourbée en crochet vers l'intérieur. A la moitié environ de sa longueur, face antérieure, une pointe secondaire aiguë se développe vers le bas. A partir de la grande courbure le membre s'amincit en feuillet, demeurant encore relativement épais, dont les bords se recourbent en gouttière tout en s'enroulant en spirale. On remarque, face inférieure, un petit talon (*a*) arrondi, peu important auquel fait suite, côté latéral externe, une excroissance lobiforme (*e*) creusée en cuillère, de forme triangulaire, à sommet aigu. Le bord opposé à la pointe, dans l'axe du corps, reste épais et sinueux et porte à la portion inférieure une longue et robuste épine coudée en angle droit (*b*) dont la pointe se dirige vers l'extrémité du membre. Extrémité distale du télopodite en feuillet aminci, enroulé en gouttière. Le bord latéral, celui conduisant la rainure séminale, continue son mouvement helicoïdal et passe sur le bord opposé latéral interne auquel il vient se souder. En examinant de face l'extrémité du membre on remarque ainsi un feuillet mince en gouttière dans lequel repose et avec lequel il se soude, le bord épais conduisant la rainure séminale.

Spirostreptus everettii Pocock, 1892 " Type "

Journ. Linn. Soc. **24** : 324.

N.W. Bornéo. R. Everett. Reg. No. 1888–122.

♂. 66 segments.

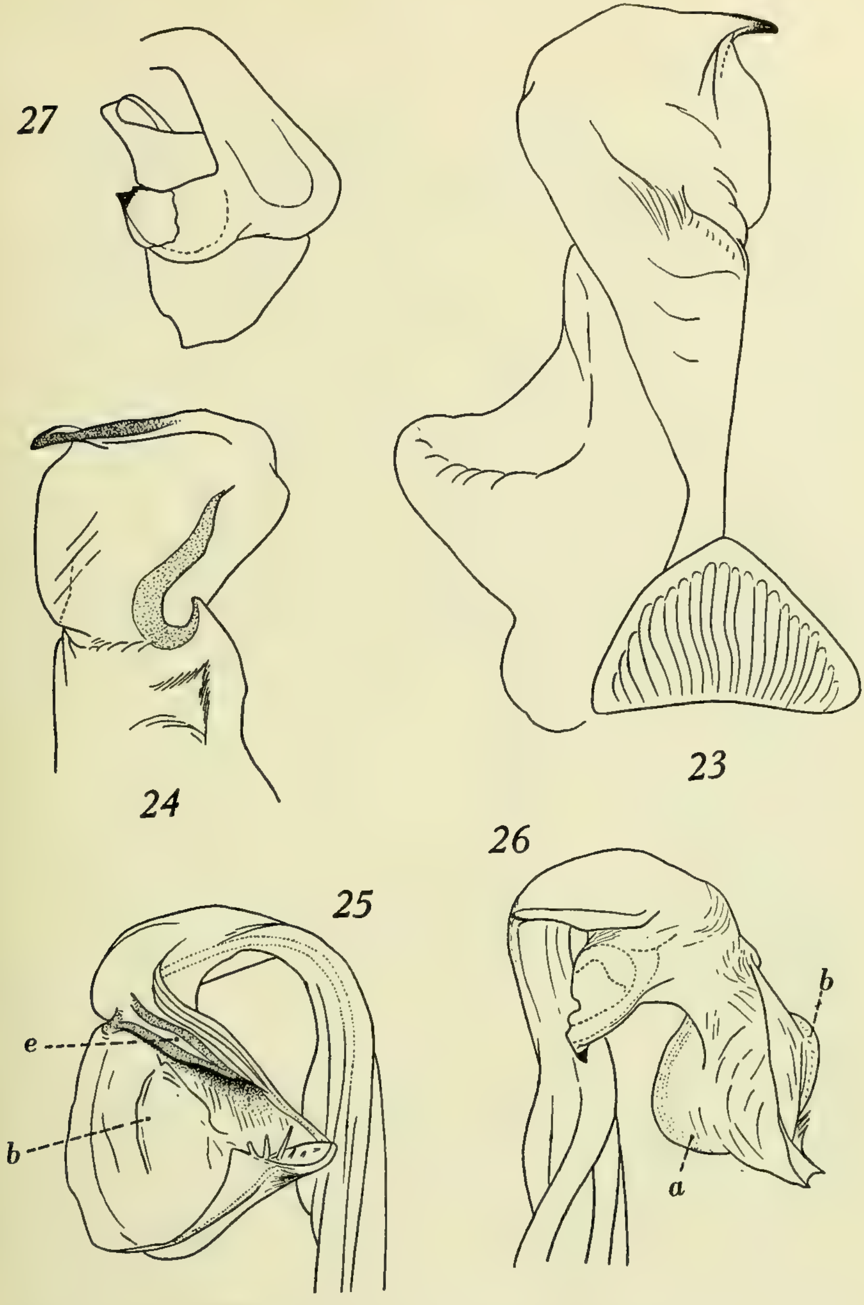
Collum en angle droit avec un large bourrelet. Pas de sillons sur la surface.

Sternite du dernier segment entièrement libre.

Cavité stigmatique allongée.

Soles sur les deux avant-derniers articles de la 4ème paire de pattes à la dernière (les 5 dernières paires de pattes sont absentes).

Pores répugnatoires débutant au 6ème segment.



Figs. 23–27. *Spirostreptus everettii* Poc. Fig. 23. Gonopodes droit, face antérieure. Fig. 24. Sommet des gonopodes, face postérieure. Fig. 25. Télopodite. Fig. 26. Télopodite. Fig. 27. Extrémité du télopodite. *a* et *b* arêtes, *e*. épine tibiale.

Gonopodes à sternite triangulaire profondément sillonné, avec une dépression près du bord postérieur.

Les organes génitaux sont légèrement abimés, la hanche droite est cassée.

Feuillet coxal postérieur très étroit (fig. 23) à la base puis rapidement épanoui en une large palette à sommet arrondi, armé d'une pointe aiguë recourbée en crochet vers l'intérieur lui donnant une forme de tête d'oiseau. Arête interne, sous le crochet, verticale, considérablement amincie, translucide, lobiforme au sommet. Surface du feuillet creusée d'une profonde dépression oblique délimitant la base de la palette.

Feuillet coxal antérieur subrectangulaire, épais à la base, avec, dans le milieu, une faible dépression. Face postérieure (fig. 24), au niveau de la soudure avec le feuillet précédent, il est profondément échancré et orné côté latéral externe d'une protubérance conique à pointe aiguë.

Télopodite (figs. 25 et 26) simple, progressivement courbé à sa sortie de la gaine coxale, à extrémité considérablement épanouie en palette arrondie, légèrement recourbée. Face inférieure de cette palette en cuillère, face postérieure fortement bombée (fig. 26) de ce fait et surmontée d'une longue arête de chitine translucide (*a*). Le fond de la dépression présente une longue crête longitudinale (*b*) (figs. 25 et 26). De la base de la palette issue de l'étranglement, limitant cette palette du reste du télopodite, une longue et large épine à pointe très aiguë (*e*). Face inférieure, à la base de l'épanouissement en cuillère, on remarque un important processus globuleux terminé par une pointe aiguë fortement colorée (figs. 26 et 27). Ce processus est une véritable ampoule dont l'extrémité distale est munie d'une ouverture semi-circulaire à bords déchiquetés.

Spirostreptus hosei Pocock, 1892 " Type "

Journ. Linn. Soc. **24** : 323.

Bornéo. Reg. No. 1889.8.5.11.

♂. 70 segments.

Lobe du collum avec angle antérieur obtus et angle postérieur saillant en arrière. Pas de sillons sur la surface.

Sternite du dernier segment complètement soudé.

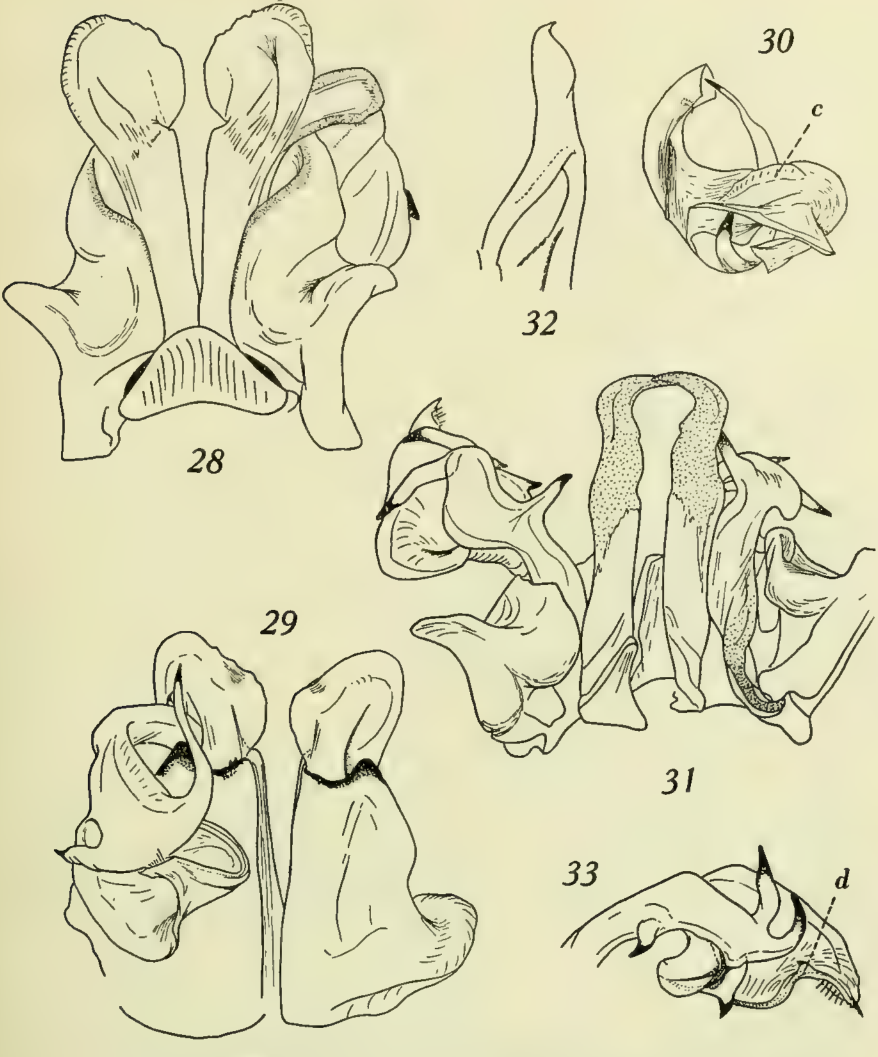
Cavité stigmatique allongée.

Soles sur les deux avant-derniers articles de la 4ème paire de pattes à la dernière.

Gonopodes à sternite en triangle de grande surface, à angles arrondis. Des stries longitudinales.

Feuillet coxal postérieur (fig. 28) très étroit à la base puis rapidement élargi vers le haut. Sommet en large palette subarrondie, en feuillet mince, soulignée à la base, près de l'arête interne, par une profonde échancrure. Côté interne très large près de la palette distale qui se soude dans son milieu.

Feuillet coxal antérieur considérablement développé, pas très étalé latéralement et bas. Une profonde dépression sur ce sommet délimitant un petit bourrelet latéral. Face postérieure (fig. 29) le feuillet est très élevé atteignant les $\frac{3}{4}$ de la longueur du feuillet précédent. Sommet pointu, en tronc de cône.



Figs. 28–33. *Spirostreptus hosei* Poc. Fig. 28. Gonopodes, face antérieure. Fig. 29. Gonopodes, face postérieure. Fig. 30. Télopodites. *Spirostreptus baluensis* Poc. Fig. 31. Gonopodes, face antérieure. Fig. 32. Hanche, profil externe. Fig. 33. Télopodite. *c*. lamelle du télopodite, *d*. denticulation distale.

Télopodite (figs. 29 et 30) court et large, progressivement recourbé à sa sortie de la gaine coxale. Une petite épine fémorale en crochet sur la courbure.

Extrémité distale largement étalée en palette semi-ronde dont la pointe, légèrement allongée, se recourbe sur elle-même et porte les épines classiques. Côté latéral du membre, à sa sortie de la gaine coxale, élargi en lame qui se replie sur la face postérieure du membre et adopte une forme en serpe. Chaque angle porte une épine d'importance différente. L'épine latérale externe robuste, courte et épaisse, l'épine latérale interne, au contraire, grêle, très allongée et sa pointe dirigée vers le sommet des hanches. Face inférieure on remarque une longue crête hyaline (*c*), épaisse, longitudinale et légèrement oblique, sous l'épanouissement distal.

Spirostreptus baluensis Pocock, 1892 " Type "

Journ. Linn. Soc. **24** : 326.

Mt. Kina Balu, Bornéo. Whitehead. Reg. No. 1960.2.2.2.

♂. 67 segments.

Collum à lobes en angle droit très arrondi. Bourrelet marginal étroit. Quelques courtes griffures près du bord postérieur.

Sternite du dernier segment soudé.

Cavité stigmatique triangulaire, allongée.

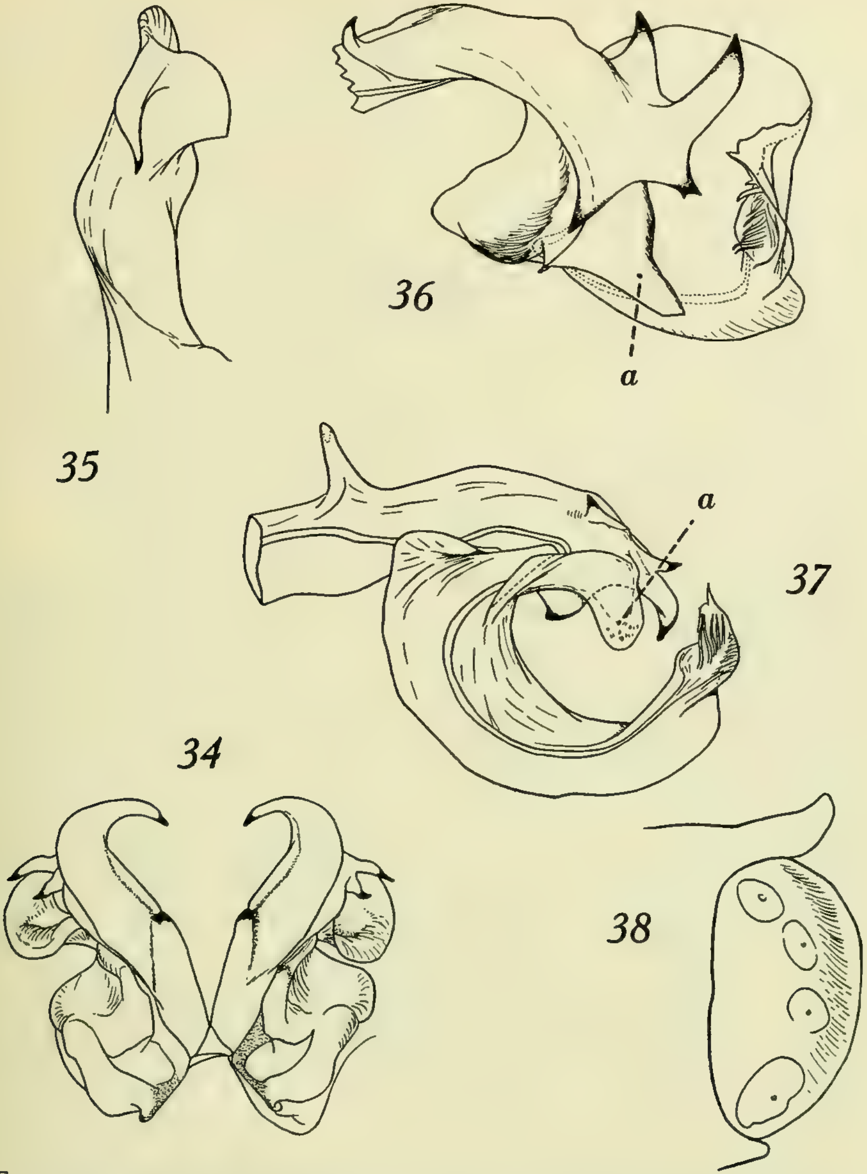
Les gonopodes sont en mauvais état et les deux hanches droite et gauche ont été légèrement écrasées à la base et séparées l'une de l'autre. Il nous a donc été impossible de donner une figure exacte de l'orifice de la gaine coxale et de la forme des gonopodes face postérieure. Néanmoins la figure telle que nous la publions est suffisante pour reconnaître l'espèce.

Gonopodes à sternite triangulaire très étroit et allongé avec un sillon longitudinal médian.

Feuillet coxal postérieur (fig. 31) ă bords latéraux à peu près parallèles, à peine sinueux ; long et étroit, à sommet en pointe aiguë recourbée en crochet vers l'intérieur. Les deux pointes se font face. Surface à peu près lisse sans dépression particulière. Face latérale interne creusée d'une profonde rigole triangulaire (fig. 32) servant de logement à la branche montante, très épaisse et sinueuse du télopodite.

Feuillet coxal antérieur peu développé en largeur et en hauteur. Latéralement la portion supérieure est creusée d'une gorge profonde. Face postérieure le bord supérieur est épaissi en un bourrelet limitant l'orifice de la gaine coxale. Nous n'avons remarqué aucune protubérance conique particulière.

Télopodite (fig. 33) court et trapu, à extrémité largement étalée en palette subcirculaire, pliée vers l'arrière et enroulée sur elle-même. Extrémité distale de cette palette armée d'une large denticulation (*d*) se dressant perpendiculairement et située à proximité de l'orifice de la rainure séminale. Au niveau d'un rétrécissement marquant le début de la palette distale, on remarque une robuste épine aiguë. Face inférieure, sous l'épine, fortement épaissie le long du bord.



Figs. 34–38. *Spirostreptus dulitianus* Poc. Fig. 34. Gonopodes, face antérieure. Fig. 35. Extrémité distale des gonopodes, profil interne. Fig. 36. Télopodite. Fig. 37. Télopodite, profil. Fig. 38. Extrémité du corps. *a*. lobe du télopodite.

Membre régulièrement arqué, épais à la base et brusquement gibbeux au niveau de l'épanouissement distal. Cette gibbosité porte deux robustes épines distales recourbées vers l'extérieur latéralement et une microscopique denticulation à la partie latérale interne au même niveau que l'épine proximale de la palette. Une épine fémorale épaisse et courte.

Spirostreptus dulitianus Pocock, 1892 " Type "

Journ. Linn. Soc. **24** : 325.

Mt. Dulit. C. Hose. Reg. No. 1892.5.29.4.

Aucune mention particulière ne désignait ce Myriapode comme type mais nous le considérons comme tel car un seul exemplaire de cette espèce a été capturé et par conséquent il ne peut s'agir que du Type.

♂. 68 segments.

Collum à lobe en angle droit, à bourrelet marginal étroit. Pas de stries sur la surface.

Sternite du dernier segment entièrement soudé. Valves (fig. 38.)

Cavité stigmatique en triangle allongé.

Pas de soles sur les pattes ambulatoires.

Gonopodes à sternite triangulaire petit.

Feuillet coxal postérieur (fig. 34) étroit et élancé, progressivement aminci en pointe et à sommet recourbé vers l'intérieure, en faucille. Sommet mince, lamellaire, à bord interne tranchant. Face postérieure épaisse dans la concavité de la courbure et relevée en lamelle épaisse placée transversalement par rapport au plan du feuillet (fig. 35).

Feuillet coxal antérieur large et peu élevé, muni d'une large gouttière arrondie, profonde, déterminant deux saillies bossues, latérale et interne, tout contre le feuillet. Ce bourrelet interne constitue le bord latéral externe de l'orifice de la gaine coxale et face postérieure se détache en tronc de cône.

Télopodite (figs. 36 et 37) sortant latéralement, court et complexe. Forme générale ramassée à extrémité épanouie en lamelle discoidale. Examinée de profil cette lamelle est recourbée sur elle-même (fig. 37), enroulée, tandis que ses bords latéraux se replient légèrement vers le dessous. A la naissance de l'épanouissement un long processus vaguement rectangulaire dirigé vers l'intérieur (*a*, figs. 36 et 37).

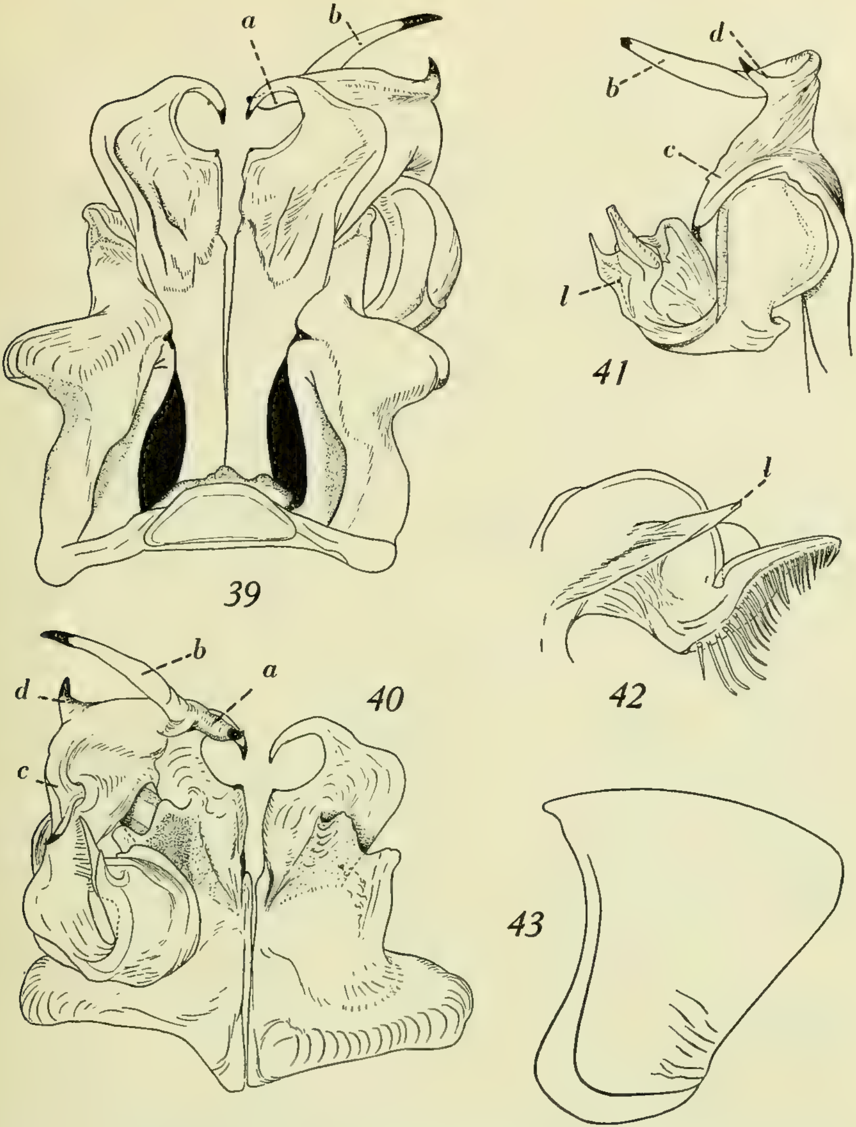
Télopodite avec une robuste épine fémorale crochue. Le long de son parcourt on remarque un fort épaississement longitudinal, comme chez *heterurus*, auquel fait suite une large pièce libre armée de 4 épines robustes (fig. 36). Cette pièce et la lamelle latérale interne (*a*) rejoignent presque l'extrémité du télopodite pour former une sorte d'anneau.

Thyropygus anurus Pocock, 1896 " Cotype "

Ann. Mus. Civ. St. Nat. Genova, **16** : 349.

Kaibii hills. Reg. No. 1895.11.10.59.

Malgré nos recherches nous n'avons pu retrouver le type de cette espèce.



FIGS. 39–43. *Spirostreptus anurus* Poc. Fig. 39. Gonopodes, face antérieure. Fig. 40. Gonopodes, face postérieure. Fig. 41. Télopodite. Fig. 42. Extrémité distale du télopodite. Fig. 43. Collum. *a, b, c, d.* épines du télopodite, *l.* lamelle.

♂. 70 segments.

Collum à lobe développé vers le bas. Bourrelet marginal volumineux et large (fig. 43).

Sternite du dernier segment libre.

Cavité stigmatique triangulaire.

Soles sur les deux avant-derniers articles de la 3ème paire de pattes à la dernière.

Gonopodes à sternite triangulaire à angles arrondis. Surface lisse.

Feuillet coxal postérieur (fig. 39) très étroit à la base et progressivement étalé en palette vers l'extrémité. Bord interne très fortement échancré au sommet produisant, à la base de l'échancrure, une petite dent mousse. A l'opposé de cette dent une longue épine mince recourbée vers le bas continuant le bord supérieur du feuillet. Surface fortement déprimée en cuillère et plus ou moins striée-striolée.

Feuillet coxal antérieur (fig. 40) très volumineux, peu développé en largeur, mais surtout en hauteur. Près de l'extrémité on constate un brusque rétrécissement correspondant au passage du feuillet face postérieure. Bord supérieur, oblique vers l'extérieur, très mince et découpé en deux dents larges et à pointe arrondie.

Télopodite (figs. 40 et 41) volumineux et complexe. Dès sa sortie de la gaine coxale le membre pousse une gibbosité très volumineuse, s'étale en feuillet épais et se replie sur lui-même tout en se courbant en angle aigu. Gibbosité de la grande courbure en forme de croissant dont la pointe antérieure pousse une volumineuse épine bifide développée horizontalement et dans le sens circulaire côté interne-côté externe et dont l'une des pointes (*a*) est au moins trois fois moins longue que l'autre (*b*). Pointe postérieure saillant en une large épine denticulaire (*c*) dont la racine est noyée dans le repli du membre. Sommet du processus avec une 4ème épine (*d*) robuste, légèrement recourbée vers l'intérieur.

A partir de la pliure le membre s'étale (fig. 41) en un épais et large lobe latéral arrondi, dont le bord conduit la rainure séminale. Après un étranglement du bord et un léger mouvement helicoïdal l'extrémité se recourbe en crochet et se creuse en un profond bonnet. Extrémité distale (fig. 42) épaissie et portant en son centre un petit appendice séminal recourbé en angle droit planté de 20 à 25 épines translucides. Sur le bord externe, à côté du rameau séminal, une longue lamelle (*l*) chitineuse horizontale pointue issue du bord et de même longueur que le rameau.

Spirostreptus oatesii Pocock, 1893 " Type "

Ann. Mus. Civ. St. Nat. Genova, **13** (33) : 404.

Double Island. Reg. No. 1892.5.4.113.120.

♂. ? segments.

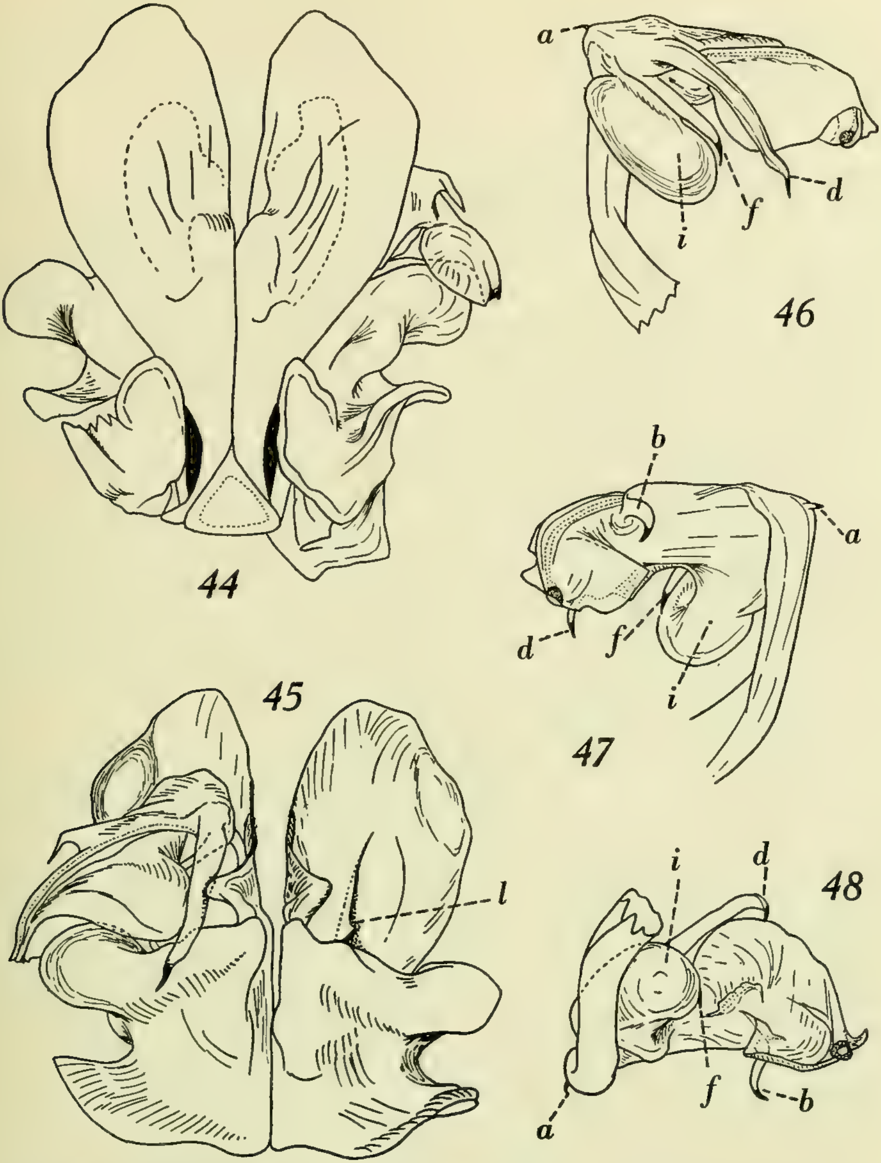
Collum avec lobes en angle droit et un large bourrelet. 4 à 5 gros plis sur la surface venant buter contre le bord marginal.

Sternite du dernier segment libre.

Cavité stigmatique triangulaire.

Soles sur les deux avant-derniers articles de la 3ème paire de pattes à la dernière.

Pores répugnatoires débutant au 6ème segment.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FIGS. 44–48. *Spirostreptus oatesii* Poc. Fig. 44. Gonopodes, face antérieure. Fig. 45. Gonopodes, face postérieure. Figs. 46, 47, 48. Télopodite. *a*. épine fémorale, *b*, *d*, *f*. épines tibiales, *i*. gibbosité du télopodite.

Nous avons trouvé un bocal contenant plusieurs individus ♂ et ♀ mais un seul a été disséqué par l'Auteur. Les gonopodes, encore attachés au segment, se trouvaient dans un tube de verre. Manifestement c'est cette pièce qui a été décrite par R. I. Pocock et nous la prenons comme type.

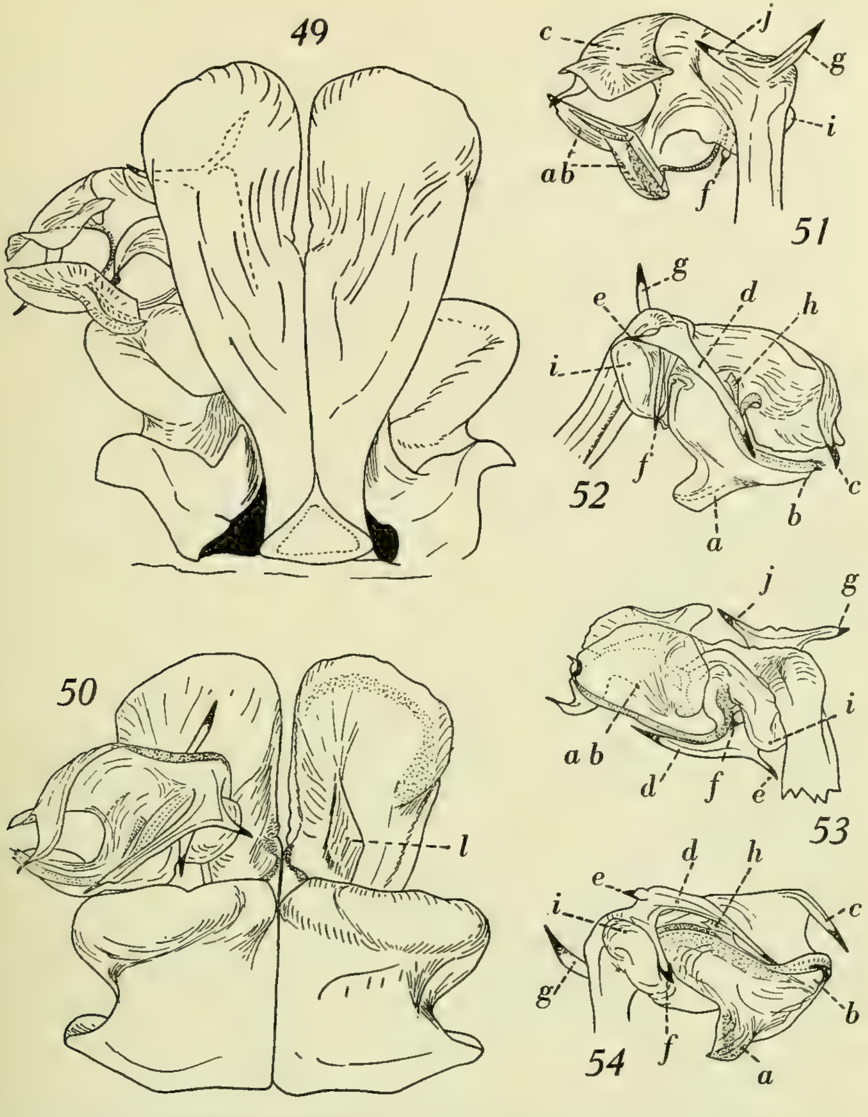
Il nous a été impossible de reconstituer le corps de l'animal les fragments de plusieurs exemplaires étant mélangés.

Gonopodes à sternite triangulaire.

Feuillet coxal postérieur (fig. 44) de forme à peu près identique à celui de *tavoiensis* mais la portion proximale est plus étroite et le sommet de la palette légèrement acuminée. Face postérieure, la lamelle limitant la face interne de l'orifice de la gaine coxale est beaucoup plus étroite. On remarque de plus que le bord interne de la fusion des deux feuillets coxaux est plus lobiforme que chez *tavoiensis* et se recourbe nettement vers l'orifice de la gaine coxale.

Feuillet coxal antérieur (fig. 45) de forme à peu près identique également à celle de *tavoiensis* mais beaucoup plus volumineux. Face antérieure, on reconnait une portion inférieure nettement délimitée par une profonde dépression de la surface du feuillet. Cette portion inférieure est elle-même fortement échancrée et possède, tout contre la base du feuillet précédent, une forte excroissance lancéolée. Portion supérieure s'élevant considérablement et brusquement tout en se courbant vers l'arrière développant une énorme excroissance dirigée latéralement horizontalement. Extrémité globuleuse de cette excroissance légèrement en crochet. Bord antérieur du feuillet fortement sinueux face postérieure. Face latérale interne, l'extrémité de ce bourrelet en balcon est limitée par une profonde échancrure en V.

Télopodite proche de celui de *tavoiensis* mais beaucoup plus simple. Grande courbure, en angle aigu, portant une minuscule épine fémorale (*a*, figs. 46–47 et 48). A partir de cette grande courbure le membre se différencie et développe un robuste tronc, gibbeux par endroit. Face inférieure, au niveau de la cassure, une gibbosité (*i*) importante, allongée et dirigée obliquement vers le bas, fortement étranglée à sa base pour abriter une longue épine (*f*). Cette épine est issue du bord latéral interne du feuillet distal, elle rencontre, face inférieure, une seconde épine beaucoup plus longue (*d*) et toutes deux s'insèrent au niveau de la grande courbure. Milieu du feuillet distal armé d'une troisième épine (*b*) plus courte, recourbée en crochet et disposée face latérale externe. Extrémité distale du télopodite étalée largement en un feuillet mince dont le lobe latéral interne est arrondi et épaissi. Lobe latéral externe conduisant la rainure séminale qui débouche dans une sorte de cuvette profonde densément colorée et dont le bord est un cercle presque parfait. A côté de cet orifice une petite lamelle hyaline. Les deux lobes du feuillet distal se recourbent vers le bas formant une large gouttière rectiligne (fig. 48). Dans le fond de cette gouttière, au sommet d'un soulèvement chitineux, une haute crête hyaline (*h*) à bord très découpé. Cette arête se développe dans le sens longitudinal et atteint presque la gibbosité de la base de la grande courbure.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Figs. 49–54. *Spirostreptus tavoiensis* Poc. Fig. 49. Gonopodes, face antérieure. Fig. 50. Gonopodes, face postérieure. Figs. 51, 52, 53, 54. Télopodite. *a.* talon de l'extrémité du télopodite, *b.* feuillet séminal, *c.* feuillet distal avec épine, *d, e, f, g, j.* épines fémorales, *h.* arête lamellaire, *i.* gibbosité du télopodite.

Spirostreptus tavoiensis Pocock, 1893 " Type "

Ann. Mus. Civ. St. Nat. Genova, **13** (33) : 405.

Reef Island. (Tavoy.) Reg. No. 1892.3.4.102.112.

♂. ? segments.

Collum comme *oatesii* mais à angle antérieur un peu plus aigu.

Sternite du dernier segment entièrement libre.

Cavité stigmatique triangulaire.

Soles sur les deux avant-derniers articles de la 4ème paire de pattes à la dernière.

Pores répugnatoires débutant au 6ème segment.

Nous avons trouvé un seul bocal contenant plusieurs individus ♂ et ♀ mais aucun " type " n'est désigné. Parmi les nombreux tronçons contenus dans ce bocal, nous avons découvert un tube de verre qui renfermait 3 segments dont le segment gonopodial. Manifestement ces segments avaient été écartés pour examiner les gonopodes. Nous pensons ne pas faire une grande erreur en annonçant qu'il s'agit des organes génitaux examinés par l'Auteur et par conséquent ceux du type. C'était d'ailleurs le seul exemplaire disséqué. Le fait que ces organes n'étaient pas détachés des segments n'est pas particulier car la systématique de l'époque n'exigeait pas un examen approfondi, le seul dessin des feuillets coxaux postérieurs suffisait. De plus R. I. Pocock n'a pas figuré les gonopodes dans son travail mais la description correspond dans tous ses détails.

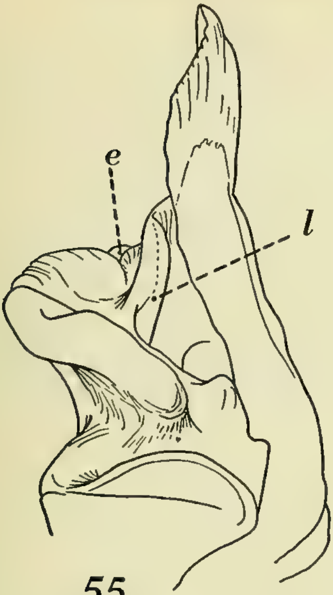
Les segments génitaux étant seuls isolés, le reste du corps mélangé aux autres individus, nous n'avons pu vérifier le nombre des segments.

Gonopodes à sternite triangulaire.

Feuillet coxal postérieur étroit (fig. 49) à la base puis progressivement élargi en une vaste palette simple, arrondie au sommet. Surface fortement déprimée dans la moitié antérieure et profondément striée. Stries irrégulières. Face postérieure, l'orifice de la gaine coxale est limitée, côté interne, par une lamelle hyaline élevée (*l*, (fig. 50). Cet orifice est d'ailleurs placé très bas latéralement. Bord interne du balcon échancré (*e*, fig. 55).

Feuillet coxal antérieur (figs. 49 et 50) volumineux et bien développé latéralement, découpé en deux portions, antérieure et postérieure, par une profonde rigole faisant tout le tour de la pièce à mi-hauteur. Première partie basse, développée latéralement. Seconde partie s'élevant progressivement tout en s'élargissant et prenant la forme d'un entonnoir très évasé. Bord épaissi et arrondi délimitant l'orifice de la gaine coxale, face postérieure, par un large balcon saillant et droit.

Télopodite volumineux, court et très complexe. La hampe montante ne se recourbe pas immédiatement mais s'élève jusqu'à l'extrémité de la lamelle du feuillet coxal postérieur (*l*) puis se courbe brusquement en angle aigu tout en devenant gibbeux. A ce niveau (figs. 51, 52, 53 et 54) et face latérale externe, jaillissent deux épines *g* et *j* dont la première, la plus longue, s'élève verticalement tandis que la seconde s'applique étroitement contre le membre. A partir de la grande courbure le membre se replie latéralement tout en s'amincissant et developpe deux processus



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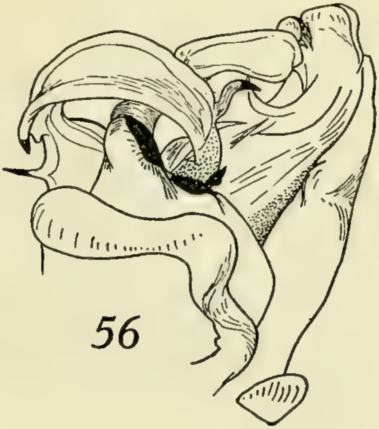

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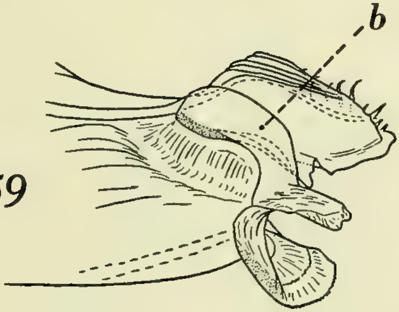

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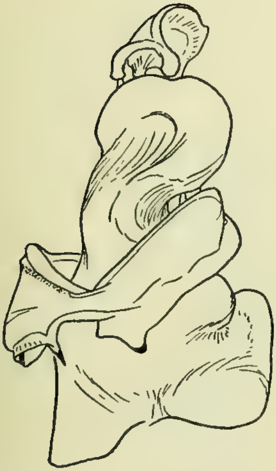

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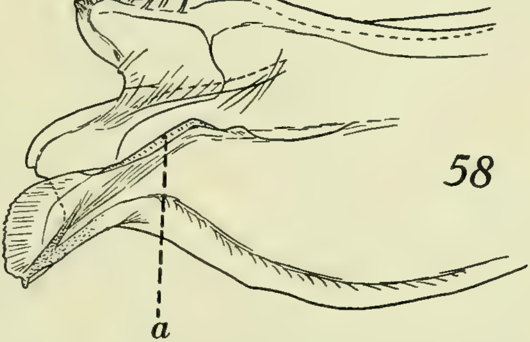

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FIGS. 55–59. *Spirostreptus tavoiensis* Poc. Fig. 55. Hanche gauche des gonopodes, profil externe. *Spirostreptus patricii* Poc. Fig. 56. Gonopode droit, profil externe. Fig. 57. Gonopode droit, face postérieure. Fig. 58. Extrémité du télopodite. Fig. 59. Extrémité postérieure du télopodite. *a*. lamelle supérieure, *b*. lamelle inférieure.

lamellaires (*b* et *c*), dont l'un conduit la rainure séminale, qui se font face comme les mâchoires d'une paire de tenailles et se développent horizontalement. Lamelle supérieure (*c*) poussant un lobe latéral externe et se terminant par une longue épine grêle. A sa base, un peu au-dessous, face latérale interne se place un processus portant trois épines dont l'une, la supérieure, est longue et se dichotomise en deux pointes, une très longue (*d*) et une petite (*e*) placée non loin de la racine. La direction de cette pointe bifide est celle du membre. La troisième épine (*f*), par contre, pousse sa pointe vers le bas et prend naissance sur le tronc du processus. Cette épine (*f*) est couchée et en partie dissimulée entre une grosse gibbosité de la lamelle inférieure (*i*) et le talon de celle-ci. Lamelle inférieure épaisse côté latéral interne (côté rainure séminale) mais très amincie et translucide, lobiforme, côté latéral externe. La partie proximale de cette lamelle est toutefois considérablement épaissie et pousse un large processus gibbeux, récurrent (*a*). Face latérale interne, entre les deux lamelles, une petite crête hyaline plantée verticalement (*h*).

Spirostreptus patricii Pocock, 1892 " Type "

Journ. Linn. Soc. **24** : 323.

Batavia. Kirkpatrick. Reg. No. 1891.4.30.8.

♂. ? segments. Corps brisé en plusieurs tronçons et écrasé.

Collum à angle antérieur un peu saillant. Bourrelet marginal épais dans l'angle. 3-4 plis et griffures légères.

Sternite du dernier segment libre.

Cavité stigmatique allongée.

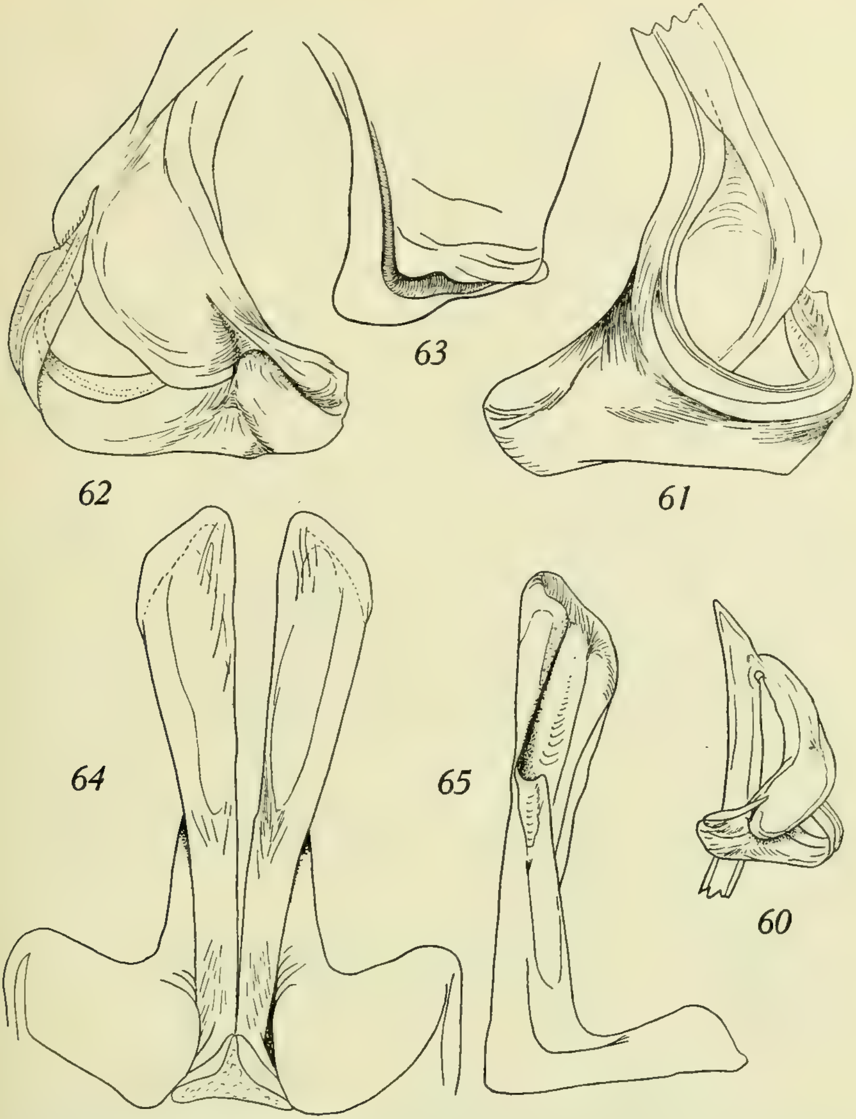
Soles sur les deux avant-derniers articles de la ? paire de pattes (pattes antérieures absentes) à la dernière.

Gonopodes ramassés à sternite en triangle isocèle à pointe arrondie. Surface irrégulièrement sillonnée.

Feuillet coxal postérieur à bord interne vertical. Bord externe légèrement épanoui latéralement en palette amincie au sommet qui dessine une large plage arrondie en cuillère recourbée vers l'arrière. Face postérieure le lobe distal est muni, dans sa concavité, d'une lamelle verticale le partageant en deux parties.

Feuillet coxal antérieur (figs. 56 et 57) en une large pièce creusée, face antérieure, d'une profonde gorge se continuant vers l'arrière. Face postérieure, feuillet large, étranglé à la base par la gorge venant de la face antérieure et au-dessus de laquelle la pièce est gibbeuse et se termine en lobe cylindrique coiffé d'une raquette globuleuse, très volumineuse fortement rabattue vers le feuillet postérieur et incliné vers la face externe (fig. 56).

Télopodite (figs. 56 et 57) épanoui en lame épaisse allongée, subrectangulaire, dès sa sortie de la gaine coxale et munie d'une saillie en pointe émoussée. Cette lame est rabattue, transversalement, sur le feuillet coxal antérieur entre la gibbosité externe et la lamelle en raquette. Près de l'orifice de la gaine une épine fémorale sinueuse grêle et courte dissimulée derrière la raquette du feuillet. Au-delà de la



FIGS. 60–65. *Spirostreptus centrurus* Poc. Type. Fig. 60. Télopodite. Figs. 61, 62. Extrémité distale du télopodite. Fig. 63. Lobe collaire. Exemplaire de M. P. Remy. Fig. 64. Gonopodes, face antérieure. Fig. 65. Hanche droite, face postérieure.

grande courbure le membre s'épanouit en plage subrectangulaire portant à son origine une épine tibiale mince et allongée. Extémité distale (figs. 58 et 59) large, découpée en deux lobes. Lobe supérieur subrectangulaire, cannelé transversalement portant 6 à 8 épines. Lobe inférieur en lamelle hyaline enroulée sur elle-même en gouttière et saillant du reste du télopodite. Le feuillet le plus externe se continue en arête perpendiculaire sur la surface supérieure de la plage (*a*). Face inférieure on remarque une deuxième lamelle (*b*), homologue, prenant naissance sur la surface inférieure près du bord interne et aboutissant sur la surface inférieure du feuillet le plus interne de la gouttière distale, face latérale. Bord du feuillet souligné d'une bande de couleur brun-rouge foncé.

Spirostreptus centrurus Pocock, 1982 " Type "

Journ. Bombay Nat. Hist. Soc. **7** : 162.

Ceylan. Holdsworth. Reg. No. 1960.2.2.3.

Nous avons trouvé un exemplaire sec de cette espèce, disséqué et ne portant aucune mention " type ". Pour nous il s'agit réellement du type.

Les organes génitaux disséqués et secs ont été brisés notamment les hanches dont le sommet a complètement disparu.

Nous avons fait subir à l'animal un traitement au phosphate trisodique afin de le ramollir et donnons ci-dessous la description des organes tels que nous les avons trouvés. Les télopodites étaient intacts et nous les représentons ici.

Nous complèterons la description et figurerons les hanches des gonopodes à l'aide d'un exemplaire de même espèce que M. le Pr. P. REMY vient de capturer lors de sa mission aux Indes. Nous le prions de trouver ici l'expression de toute notre reconnaissance pour nous avoir permis de faire une étude complète de cette espèce fort mal connue.

♂. 66 segments.

Collum à angle antérieur du lobe fortement saillant. Bourrelet marginal large, souligné, au niveau de l'angle antérieur, par une très profonde dépression (Text-fig. 63).

Sternite du segment postérieur libre.

Cavité stigmatique triangulaire.

Soles sur les deux avant-derniers articles de la 3ème paire de pattes à la dernière.

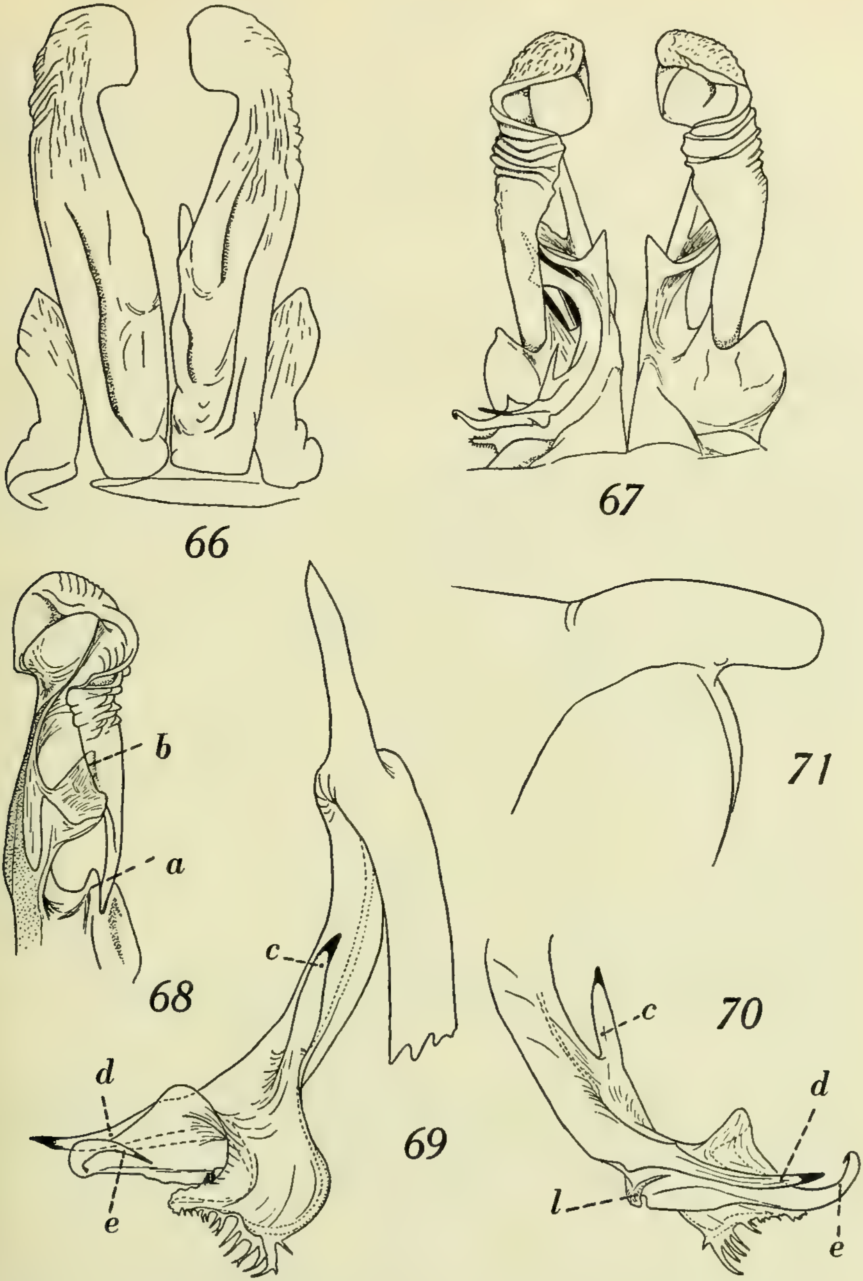
Pores répugnatoires débutant au 6ème segment.

GONOPODES.

Feuillet coxal postérieur incomplet.

Feuillet coxal antérieur large et développé latéralement avec une profonde gorge supérieure déterminant un cône latéral élevé, volumineux. Face postérieure le feuillet est simple, élevé, à sommet taillé en pointe.

Télopodite (figs. 60, 61 et 62) grêle courbé en angle aigu dès sa sortie de la gaine coxale. Au niveau de la grande courbure une longue et épaisse épine fémorale droite, dirigée vers le haut. Dès la grande courbure le membre se développe en un large feuillet enroulé en gouttière. Il est remarquable de noter que les deux bords



Figs. 66–71. *Rhynchoproctus proboscideus* Poc. Fig. 66. Gonopodes, face antérieure. Fig. 67. Gonopodes, face postérieure. Fig. 68. Extrémité du gonopode droit. Fig. 69. Télopodite. Fig. 70. Extrémité distale du télopodite. Fig. 71. Extrémité postérieure du corps. *a*. denticulation de la gaine coxale, *b*. pointe du tablier, *c*, *d*, *e*. épines du télopodite, *l*. lamelle du télopodite.

latéraux de ce feuillet prennent naissance à la partie supérieure du membre (fig. 61). Les deux bords divergent dès leur origine et s'enroulent l'un autour de l'autre. Bord latéral externe s'allongeant pour donner naissance à un rameau séminal à bords minces, lamellaires. Bord latéral interne poussant une excroissance lobiforme concave vers l'intérieur, en cuillère se soudant à la partie inférieure de la gouttière qui s'allonge vers l'avant tout en se redressant légèrement vers le haut et portant, latéralement, une gibbosité en amande.

Mâle récolté par M. le Pr. P. REMY

Ceylan. Jardin de Nuwara Eliya, 2.100 m. altitude. VIII.59.

70 segments.

Sternite des gonopodes triangulaire, très étroit à la pointe et élevé. Surface irrégulière.

Feuillet coxal postérieur (fig. 64) étroit, élancé, progressivement élargi en palette étroite, à surface régulièrement striée. Sommet arrondi. Face postérieure (fig. 65) à bord latéral externe brusquement recourbé. Surface postérieure du sommet creusée d'une profonde gouttière longitudinale dans laquelle se loge la grande courbure du télopodite surmontée d'une épaisse et longue épine fémorale. La gouttière est entièrement occupée par cet appareil.

Feuillet coxal antérieur (fig. 65) bien développé latéralement saillant à l'extrémité externe en un cône large et arrondi. Bord interne, le long du feuillet précédent, profondément cannelé. Sommet élevé, très rétréci, muni face postérieure d'une profonde échancrure déterminant une pointe mousse latérale. Sous l'échancrure une dépression longitudinale en gouttière.

Rhynchoproctus proboscideus Pocock, 1894 " Type "

Max Weber—Zool. Ergeb. III : 386.

Luwu (Celebes). M. Weber. Reg. No. 1896.10.6.80.

♂. 69 segments.

Collum à lobe en angle droit.

Sternite du dernier segment libre. Segment terminal (Text-fig. 71).

Soles sur l'avant-dernier article de la 3ème paire de pattes à la dernière.

Cavité stigmatique triangulaire.

GONOPODES sans sternite.

Feuillet coxal postérieur (fig. 66) très allongé, étroit, à bords subparallèles, légèrement étranglé près de l'extrémité. Sommet élargi et courbé vers l'intérieur en capuchon dirigé vers l'arrière. Surface finement striée dans le sens longitudinal surtout dans les $\frac{2}{3}$ proximaux. Une profonde rainure sublatérale externe déterminant un épais et large bourrelet longitudinal. Une faible dépression longitudinale dans le milieu. Sommet ridé. Face latérale externe avec fortes cannelures, près du sommet, se continuant face postérieure où le feuillet dessine un large lobe subtriangulaire rabattu sur l'ouverture de la gaine coxale. Seul le bord latéral externe se développe ainsi en large feuillet. Le bord interne se limite à la face antérieure sans expansion d'aucune sorte. Face postérieure le sommet est en profond capuchon.

Feuillet coxal antérieur (fig. 67) considérablement moins volumineux et étroit en forme de fer de lance. Sommet pointu. Postérieurement le bord latéral externe dessine d'abord une longue protubérance aiguë (*a*, fig. 68) puis s'échancre et se développe en hauteur tout en amorçant un léger mouvement de torsion. L'extrémité de ce processus dominant la première pointe externe (*a*) s'étale en une sorte de balcon disposé horizontalement et enroulé en gouttière. La portion latérale externe se développe en une large pointe placée dans la concavité du feuillet postérieur (*b*) tandis que la portion latérale interne dessine une seconde pointe plus courte.

Télopodite (figs. 69 et 70) long et mince débouchant au dehors entre le processus supérieur en balcon et la pointe proximale externe (*a*). Immédiatement ă sa sortie le membre se recourbe en angle aigu et porte une longue épine fémorale entièrement dissimulée en arrière du balcon supérieur. La grande courbure se heurte également à ce processus.

Extrémité du membre épanouie en un large feuillet de forme légèrement hélicoïdale conduisant la rainure séminale le long du bord externe qui se développe exclusivement latéralement. Portion distale de ce feuillet amincie et recourbée en crochet. Son bord postérieur porte une dizaine d'épines translucides dont les premières sont plus ou moins rassemblées en rameaux. Une (*c*) récurrente de dimension moyenne à la base de l'épanouissement distal et deux autres beaucoup plus longues au bord opposé à cet épanouissement ; une courbe externe (*d*) un peu en retrait et une très longue (*e*) inerme. L'épine interne (*e*) est de beaucoup la plus longue, se recourbe en crochet et la racine se trouve en fait au même niveau que le bord de la palette distale. Face inférieure de cette longue épine parcourue dans le sens longitudinal par une petite lamelle hyaline se heurtant à un petit lobe (*l*) lamellaire, translucide, planté transversalement par rapport à elle.

Spirostreptus vittatus Newport

Détermination de R. I. POCOCK. Penang (2.500 pt), S. Flower. Reg. No. 1896.6.20.51.

On ne connait pas de figures des gonopodes de cette espèce, à part celles publiées par CARL et POCOCK. Celles-ci sont par trop imprécises et c'est pour cette raison que nous publions la description et les dessins des organes génitaux de cet exemplaire.

♂. 80 segments.

Collum à lobe en angle droit légèrement saillant. Bourrelet marginal large, beaucoup plus large au niveau de l'angle. 2 rides environ près du bord postérieur.

Sternite du dernier segment libre.

Cavité stigmatique triangulaire.

Soles de la 3ème paire de pattes à la dernière sur les deux avant-derniers articles. Seule la 3ème paire de pattes possède des soles uniquement sur l'avant-dernier article.

GONOPODES sans trace de sternite.

Feuillet coxal postérieur large (fig. 72) et haut à bords latéraux subparallèles. Vers le sommet le bord entier s'échancre légèrement tandis que le bord distal se recourbe en crochet vers l'intérieur. Celui-ci est profondément échancré. Face postérieure le feuillet est en gouttière dans la moitié distale environ, l'orifice de cette gouttière, face latérale interne, faisant vis à vis à son homologue. Bord latéral du feuillet, face postérieure (fig. 73) considérablement épanoui en un lobe épais se repliant vers le bord interne déterminant ainsi une profonde gouttière s'ouvrant face interne. Fond de cette gouttière, vers le sommet de la hanche, soulevée par une longue arête se développant progressivement et saillant au delà du bord du feuillet. Cette arête produit ainsi à l'extrémité de la hanche deux larges encoches séparées par une longue pointe médiane.

Feuillet antérieur (fig. 73) étroit peu développé latéralement. Face postérieure il se continue par une large denticulation externe et un petit processus en forme de massue situé contre le bord de l'orifice de la gaine coxale. A ce niveau se développe, près du bord latéral interne, un complexe appareil reposant sur un étroit pédoncule et s'épanouissant en balcon horizontal. Bord postérieur de ce processus globuleux, épais mais s'amincissant rapidement en feuillet transparent subrectangulaire dont le côté externe et l'angle postérieur s'allongent en pointe ; cette dernière se glissant sous le bord latéral lobiforme du feuillet coxal précédent. On remarque une profonde échancrure en V côté latéral interne.

Télopodite (fig. 74) grêle et allongé. Branche montante atteignant le processus coxal en balcon avant de se recourber en angle aigu. Grande courbure surmontée d'une longue et épaisse épine fémorale qui se dissimule entre le feuillet coxal postérieur creusé d'une rigole et le processus en balcon. Au delà de la grande courbure le membre s'élargit progressivement, se recourbe en demi-cercle et développe un large feuillet vaguement triangulaire dont la surface inférieure, près du bord interne, porte de nombreuses cannelures élevées. Le long de ce même bord interne, on rencontre une large épine récurrente et une petite denticulation. Extrémité distale externe (fig. 75) prolongée par un délicat processus acuminé, rabattu vers le bord opposé. 3 à 4 épines translucides autour de l'orifice de la rainure séminale. Bord latéral externe, le plus épais, à surface inférieure soulevée et armée d'un robuste processus en forme de faucille s'opposant au processus séminal.

Spirostreptus feae Pocock, 1893 " Type "

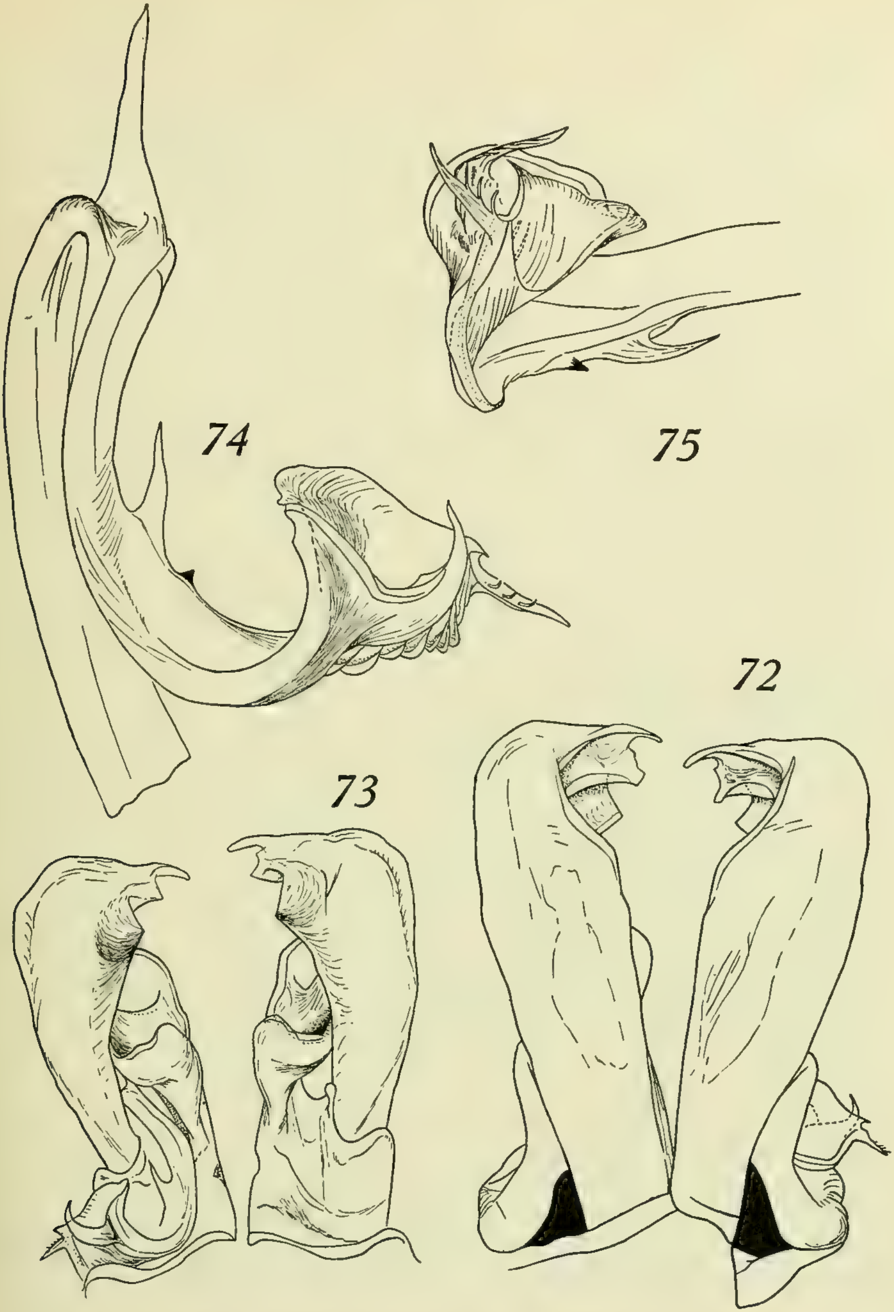
Ann. Mus. Civ. St. Nat. Genova, **13** (33) : 402.

Rangoon. Oates. Reg. No. 1892.5.4.77.78.

Nous avons trouvé dans le bocal marqué " type " deux individus complets ♂ et ♀ et un tube de verre contenant des gonopodes isolés qui manifestement sont ceux du type décrit par Pocock. Ils correspondent exactement à la description publiée.

Ce sont ces organes que nous décrivons et figurons comme type. Les caractères de morphologie externe ont été tirés des deux exemplaires ♂ et ♀ non disséqués.

Nous devons faire état au sujet de cette espèce d'un grave problème. En effet, nous possédons au Muséum National de Paris 3 individus étiquettés *feae* de la main de Pocock et portant la mention " exemplaire type " Palon Birmanie 1885-89.



Figs. 72–75. *Spirostreptus vittatus* Newp. Fig. 72. Gonopodes, face antérieure. Fig. 73. Gonopodes, face postérieure. Fig. 74. Télopodite. Fig. 75. Extrémité du télopodite.

Viaggio L. FEAE. Ces exemplaires (1 ♂, 2 ♀) ont été offerts par l'Auteur à H. W. BRÖLEMANN mais il s'avère qu'ils appartiennent à une espèce totalement différente de celle de Londres (proche de *Thyroglutus astutus* Att.). Notons que la description publiée correspond aux exemplaires du British Museum tandis que les gonopodes et plusieurs caractères de morphologie externe, notamment le nombre de paires de pattes et le sternite du segment terminal montrent que les individus du Muséum de Paris n'ont pas été examinés par l'Auteur bien que les classant *feae*.

♂. 72 segments.

♀. 73 segments.

Collum à lobe saillant chez le ♂ (fig. 80) en angle droit chez la ♀ (Text-fig. 81). Sternite du dernier segment pedifère soudé.

Soles sur les deux avant-derniers articles de la 3ème paire de pattes à la dernière.

GONOPODES sans sternite.

Feuillet coxal postérieur (fig. 76) large et élancé, étroit à la base et épanoui distalement en palette arrondie à l'extrémité. Les deux hanches sont légèrement tordues vers l'intérieur dos à dos. Surface peu sculptée.

Feuillet coxal antérieur de faible volume, triangulaire face antérieure et médiocrement développé latéralement. Face postérieure le feuillet s'élève très rapidement vers la bord interne et s'épanouit à son extrémité en un large lobe (figs. 77 et 78) subrectangulaire à bords irréguliers rabattus horizontalement vers l'arrière et recourbé obliquement vers la base des gonopodes. Bord latéral de la lamelle largement et profondément échancré en rond. Près du bord postérieur, c'est-à-dire celui faisant face à l'observateur, surface profondément déprimée en entonnoir, le bord lui-même orné d'une grande lamelle hyaline verticale dominant la dépression. Cette dépression est compensée, face inférieure, par une forte boursouflure conique.

Télopodite (figs. 77 et 79) très simple et grêle à branche montante atteignant la lamelle du feuillet coxal qui forme toit et se recourbant brusquement en angle aigu. Epine fémorale de la courbure grande et épaisse, se développant verticalement, logée, ainsi que la branche montante, dans une gorge en gouttière verticale et dépassant le processus coxal en toit.

Reste du membre long et grêle armé à mi-parcours d'une longue et robuste épine dont la pointe se dirige vers le bas.

Extrémité distale du télopodite étalée en une plage hyaline dont le bord est armé d'une douzaine de pointes transparentes.

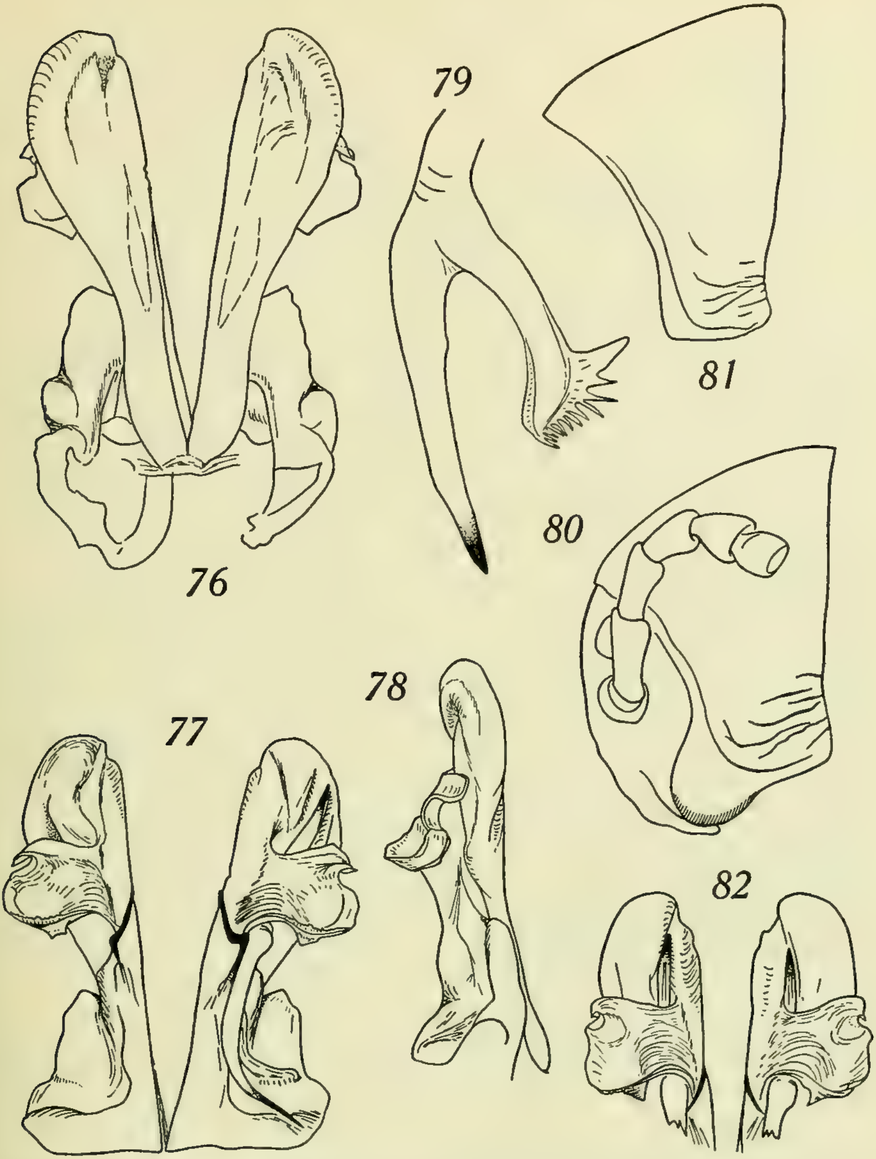
Les gonopodes de l'individu ♂ à 72 segments présentant une légère différence dans la forme de la lamelle coxale nous les figurons ici (fig. 82).

Spirostreptus gestri Pocock, 1893 " Type "

Ann. Mus. Civ. St. Nat. Genova, **13** (33) : 402.

Plapoo. Mt. Mooleyit. Fea. Reg. No. 1895.11.10.54.

Le bocal contenant cette espèce portait l'étiquette *Thyropygus gestri* Poc., nous pensons que l'Auteur a changé cette espèce de genre sans en publier les raisons. L'étiquette originale était bien *Thyropygus*. D'autre part, la mention " type "



Figs. 76–82. *Spirostreptus feae* Poc. Fig. 76. Gonopodes, face antérieure. Fig. 77. Gonopodes, face postérieure. Fig. 78. Hanche gauche, profil externe. Fig. 79. Extrémité du télopodite. Fig. 80. Tête et collum du ♂. Fig. 81. Collum de la ♀. Fig. 82. Extrémité des hanches des gonopodes du second exemplaire.

n'était pas indiquée mais le seul individu ♂ présent et disséqué ainsi que la station correspondant à la publication nous le font désigner comme tel.

♂. 65 segments.

Collum à lobe en angle droit avec un gros bourrelet marginal surtout élargi dans l'angle antérieur.

Sternite du segment terminal libre.

Cavité stigmatique triangulaire.

Soles sur les deux avant-derniers articles de la 3ème paire de pattes à la dernière.

Pores répugnatoires débutant au 6ème segment.

Gonopodes à sternite trapezoidal, lisse.

Feuillet coxal postérieur (Text-fig. 83) très étranglé à la base puis progressivement élargi et épanoui en lamelle au sommet. Cette lamelle est de forme semi-circulaire, déprimée en son centre sur les deux faces (Text-fig. 85) et rabattue verticalement de façon à se disposer perpendiculairement à l'axe de la hanche. La partie circulaire est dirigée vers l'avant, la portion droite continuant le bord interne de la hanche qui est sinueux demeurant ainsi dans le plan général de l'organe et produisant un léger ressaut distal duquel est issue une petite lamelle perpendiculaire située antérieurement. Le bord aminci du processus est lamellaire et irrégulièrement dentelé. Face postérieure (fig. 84) et correspondant à la pliure longitudinale du lobe distal, on remarque un tronc épais, plus ou moins bossu, s'évasant vers le bas.

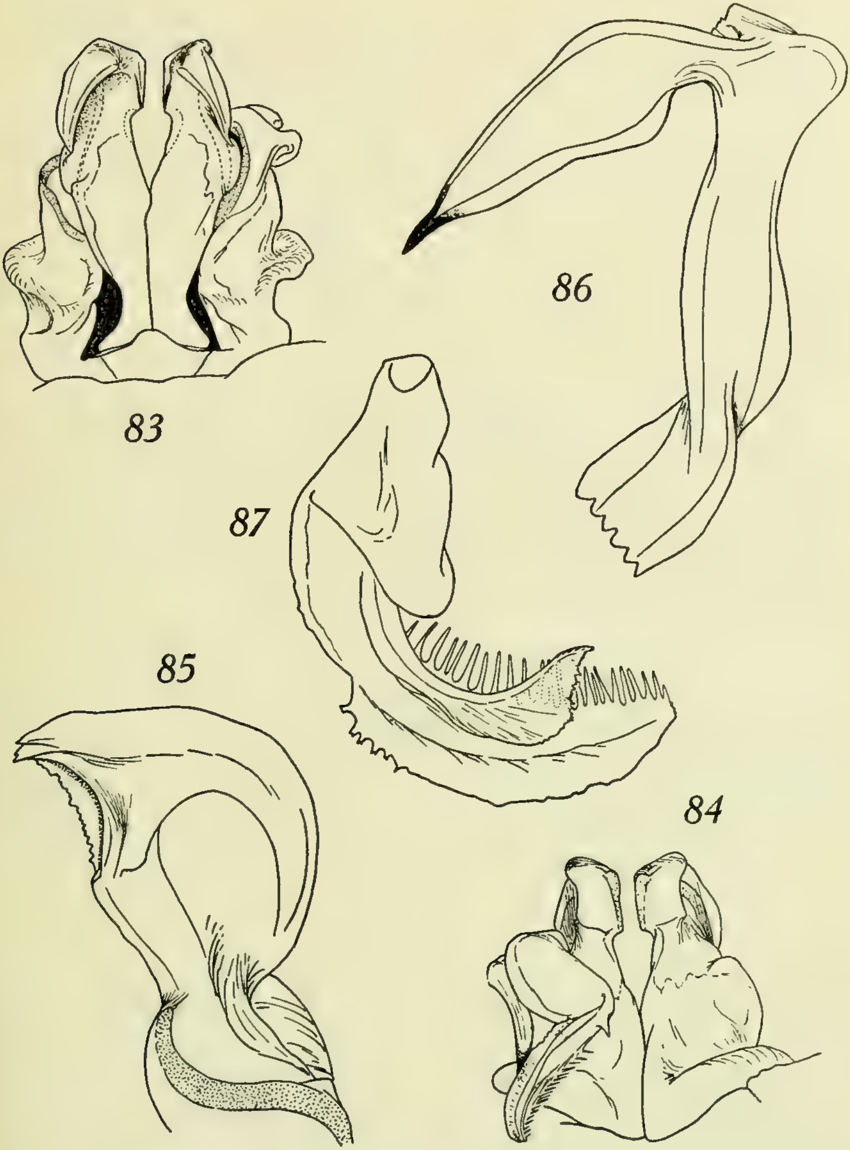
Feuillet coxal antérieur (fig. 84) élevé et creusé latéralement d'une dépression classique faisant le tour de l'organe. Face postérieure, avant et au niveau de sa jonction avec le feuillet précédent, le bord est épanoui en un large lobe latéral.

Télopodite court et relativement simple. Branche montante épaisse et brusquement rabattue en angle aigu dès sa sortie de la gaine coxale. A partir de la grande courbure le membre s'épanouit en large et épaisse lamelle semi-lunaire dont l'extrémité étranglée pousse un long processus tout en s'amincissant et en se recourbant en angle droit. Ce processus (fig. 84 et 87) dont les bords sont lamellaires et transparents porte, le long de son bord, une série de pointes fragiles et translucides au nombre de 22 à 23 et présente au bord latéral interne, au niveau de la courbure en angle droit, une denticulation hyaline. Dans le milieu de l'appareil, face inférieure, (fig. 87) on remarque, étroitement accolée à sa surface, une petite lame à bord distal nettement dentelé et conduisant la rainure séminale. Nous sommes donc en présence d'un télopodite bifide dont, des deux branches, l'une conduit la rainure, l'autre porte les épines.

Au niveau de la grande courbure, latéralement et un peu au-dessous de l'épaississement lobiforme, une très robuste et large épine dont la pointe se dirige vers l'extrémité du membre (fig. 86).

Spirostreptus stenorhynchus Pocock

Nous avons examiné deux ♂ et deux ♀ mais n'avons pas trouvé de type désigné. Nous ne sommes pas certain que l'un des ♂ soit le type bien qu'un seul ait été disséqué.



FIGS. 83–87. *Spirostreptus gestri* Poc. Fig. 83. Gonopodes, face antérieure. Fig. 84. Gonopodes, face postérieure. Fig. 85. Sommet du gonopode gauche de profil. Fig. 86. Epine fémorale. Fig. 87. Extrémité distale du télopodite.

Pour cette espèce la description et les dessins ont moins d'importance que pour les autres espèces étudiées car depuis Carl elle est bien connue et figurée.

Les segments, pour ces individus, sont au nombre de:

♂: 53,53.
♀: 61,33 ?

Thyropygus erythropleurus Pocock, 1894 " Type "

Max Weber—Zool. Ergeb. III : 384.

Manindjau, Sumatra. Weber. Reg. No. 1896.10.6.78.

Cette espèce a une importance très grande car elle a été désignée comme type du genre par Pocock.

Malheureusement le matériel ayant servi à l'Auteur n'est constitué que par 2 ♀ et un jeune ♂.

Nous n'avons retrouvé comme type qu'une ♀ qui est bien caractéristique avec ses points jaune-rouge près des pores répugnatoires et son corps annelé de marron-rouge et blanc-jaune sale. Les pattes sont également très distinctement annelées de même couleur.

En l'absence de ♂ adulte et dans l'état actuel de nos connaissances des ♀ nous ne pouvons que suivre les Auteurs qui ont désigné l'espèce *javanicus*, la plus ancienne décrite et la plus commune, pour la remplacer.

SUMMARY

The object of this paper is to redescribe and figure R. I. Pocock's species of Harpagophoridae represented in the Collections of the British Museum (Natural History).

Although Pocock described thirty-two species, I have been able to deal in detail with only seventeen of them. The remainder are either not represented in the Collections or are represented only by females, or by females and young males.

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A PROPOSED RECLASSIFICATION OF THE GASTROPOD FAMILY VERMETIDAE

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-2 MAR 1961
PRESENTED

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ABSTRACT

Because of their widespread occurrence in the intertidal zones of warm-temperate to tropical seas and their peculiar adaptations, the Vermetidae could become useful to the marine ecologist if they were readily identifiable in the field. The present paper is an attempt to show what characteristics are most constant and useful in recognition, to review the nomenclatural history of the group, and to indicate something as to the geographic distribution of species. In the revised classification, five genera, with five additional subgenera, are recognized. Brief lists of the species that may be assignable to each are given, although these must remain tentative until detailed studies are made by students who have access to properly collected material.

In this paper, *Tripsycha* is proposed as a new genus ; *Siphonium lituella* Mörch is selected as the type species of *Dendropoma* Mörch, *Serpulorbis polyphragma* Sassi as that of *Thylacodes* Mörch, and *Bivonia contorta* Carpenter as that of *Thylacodus* Mörch and of *Thylaeodus* Mörch ; and lectotypes are selected for *Vermetus adansonii* Daudin, *V. afer* Gmelin, *Bivonia contorta* Carpenter, *B. c.* var. *indentata* Carpenter, *Petaloconchus macrophragma* Carpenter, *Siphonium* (*Dendropoma*) *leucozonias* Mörch, and *Siphonium* (*D.*) *lituella* Mörch.

A. INTRODUCTION

THE Vermetidae (worm gastropods) probably hold a record among molluscs for the degree of confusion they have promoted, both in collections and in the literature ; for they have been misconstrued at every level from subspecies to phylum. An attempt is made here to point out objective criteria for separation of groups within the family. A complete monograph of the species, however, must wait until field observations have confirmed or disproved laboratory analyses of seeming differences.

Although in many parts of the world—especially in the tropics—the vermetids are abundant intertidal organisms, they have never been popular with collectors. Properly recognized, they could become, on account of their peculiarities in habit and distribution, useful indicators for the ecologist in the description of intertidal zones. Most of the few papers on the family deal with anatomy and physiology of the animals or with local faunas. We still lean upon the systematic reviews by two authors whose works were published a century ago: Carpenter (1857*b*), for a monograph of the genus *Petaloconchus*, and Mörch for, first, a tentative classification of the family (1859–60*a*) and then (apparently after a survey of the extensive Hugh Cuming Collection) a review of the species (1861–62*b*). His second arrangement differs at many points from the first one. Conceptual tools for the study of variation had not been worked out in Mörch's time. Small wonder, then, that in trying to cope with some of the most variable of gastropods he finally resorted to a naming system so complex and confused that Carpenter (1864 : 558, footnote) later dismissed it as a "posture of binomial nomenclature". Indeed, one now concedes that, useful as Mörch's work may be in a general way, we must, under modern rules, reject many of the new names he proposed, for all those below specific rank are polynomial and inconsistent. Citation by Tryon (1886) and reprinting by Clessin (1901–04) were not in a form that would validate any of them.

Both Mörch and Carpenter relied upon the adult shells alone for their classifications. Perhaps neither had an adequate microscope, for they both missed some conspicuous features in the nuclear whorls, and Mörch saw structures in certain opercula that later research has failed to confirm.

The first step in a fresh study of the family is to define its limits and to exclude what does not properly belong. Tubicolous annelid worms are frequently confused with vermetids. Some of these worms do build irregularly coiled tubes, but on close inspection one sees that the tubes are lustreless and of two-layered construction, either beginning with a non-coiled initial chamber or open at the posterior end. The genera *Burtinella*, *Discovermetulus*, *Lemintina*, *Serpula*, *Spirorbis*, *Tubulostium* and *Vermilia* may be rejected without hesitation, for their type species are now generally recognized as annelids. Although from time to time authors have listed *Caporbis*, *Segmentella*, *Serpulus*, *Stoa*, and *Spiroglyphus* as gastropods, these groups also should probably be classed as annelids. At the family level, the Vermetidae have been traditionally associated with *Vermicularia*, a group that Morton (1953) has shown to be related rather to Turritellidae, for the juvenile shell is coiled in much the same general plane as the later whorls. *Stephopoma* and *Siliquaria*, also with turritelloid apices, belong near *Vermicularia*.

Remaining in Vermetidae, then, are those forms, solitary or colonial, in which the juvenile snail, upon emergence from the capsular membrane and the protection of the parent's tube, attaches itself to a favourable substrate and begins coiling its adult shell around an axis at a 90° angle to that of the larval shell. Several named genera may be recognized, combining differences in anatomical and shell structures, manner of coiling, and habits. The present paper will attempt to subdivide the restricted family Vermetidae in terms of the hard parts and general external aspects, while a paper by Dr. Morton, to be published later, will discuss differences in anatomy and feeding patterns.

The Vermetid Shell

An isolated section of a vermetid tube is nearly useless for specific or even generic determination, but texture and structure may indicate its placement within the family. The shell is three-layered, with an inner layer that is glossy and porcellanous, mostly white or tinged with some shade of brown. The middle layer is less distinctive but thicker than the other two, and the outer layer carries whatever sculpture is present, its colour ranging from white through buff or pink to brownish black. Sculpture may be either longitudinal or transverse. The irregular coiling of the shell makes the use of such terms as "spiral" and "axial" ambiguous. Full expression of sculpture may be inhibited by such factors as crowding, rate of growth, and unfavourable environment, which adds to the problems of recognition. Several writers have commented on the frequent sealing off of the early whorls, especially if the shell has been broken. The posterior part of the mantle is capable of secreting a convex septum that closes off either an unneeded or a broken portion of the tube, and in some specimens this sealing may be repeated at close intervals. In one genus (*Petaloconchus*) one or more spiral laminae or shelves may encircle the columella throughout the medial whorls.

The Operculum

The operculum is a spirally-wound plate of chitin. At its most complex development it is thickened at the centre, with a button-like scar on the inner surface, the spiral so tightly appressed as to seem nearly flat. An intermediate or simple form of operculum shows only a few turns, the whole structure reduced in size to half or less of the diameter of the aperture, with spirals that stand up as coiled laminae on a saucer-shaped base. One group of the vermetids (*Serpulorbis*) has dispensed with the operculum entirely. Correlations of opercular patterns with feeding habits will be discussed by Dr. Morton.

The Nuclear Whorls

Few gastropods are adapted to a sessile existence. Perhaps this accounts for the vermetids having developed a special means for the newly-emerged young to cement their shells to the substrate without becoming imprisoned in the process. The larval shell is comprised of two to four normal-appearing whorls except that the aperture is either twisted forward or provided with a sinuous or almost clawlike outer margin. So shaped, the shell can lie firmly against the substrate while the animal continues both feeding and the formation of the next volutions of the shell, which encircle the juvenile shell on an axis of coiling 90° different from that of the initial whorls. This is reminiscent of the submerged nucleus in Architectonicidae, to which group the Vermetidae may be related.

Nuclear whorls may be found in three ways: (*a*) By scanning the underside of a colony or an individual coil broken loose from the substrate; (*b*) by inspecting the outer surfaces of adult tubes—especially crevices near the apertures—for newly-emerged young that creep down the outside of the parent's tube and attach in the first protected niche they encounter; (*c*) by extracting the soft parts from adult tubes (especially from those that have been quickly dried after collection or preserved in neutral alcohol) for the young or larval shells that may still be sheltered in the mantle cavities of the adults. With practice one soon learns to recognize the newly-attached young, which may be detected even with a small hand-lens. At first glance they look like a plump little wheel of an automobile, with a shiny central cap.

Under higher magnification, differences become apparent, as one compares the young of groups here called genera for size, number of nepionic whorls, colour, and relative shape.

Habits of Growth

It is impossible to arrive at any generalizations as to growth patterns that will apply to every contorted mass of vermetids that one finds. Nor is it even possible to identify every such mass, a fact that accounts in part for the unpopularity of the family with collectors. However, there are some features for which one should watch. Are the tubes entrenched in the substrate or slotted into each other where one overrides another? Is coiling rather regularly planorboid during the earlier part of the adult whorls? Are the whorls uniformly small and coiled like a " *Turritella* squeezed sideways "? Are there fairly regular scars of broken tube ends, where a vertical feeding tube has been abandoned and replaced by one taking off at a different angle? It is this sort of pattern that may give a clue as to generic placement, but confirmation should be sought in the other characteristics. One group, *Petaloconchus*, has an internal structure that is a sure clue—spiral laminae of complex form that project into the tube from the columellar wall. The function of these structures is yet open to investigation. Another problem that remains for future solution is the relationship between form of shell and the degree of crowding in colonies. Is solitary versus colonial development a specific character? Or do isolated individuals producing young inevitably form a tight-knit colony? No one has yet performed the observational experiments that would give the answer, or at least no published record has come to our attention.

Some of the early authors, especially Mörch and Carpenter, thought that many vermetids were sinistrally coiled, but this seems to be a matter of faulty observation, for no sinistral specimens have been seen during the course of the present study, which has involved scrutiny of hundreds of specimens over a period of some ten years. Probably the 90° change of angle, which they failed to note, may have led to this impression. Also, they, like other authors, may have mistaken specimens of *Spirorbis*, an annelid worm that coils either way, as vermetids.

B. NOMENCLATURAL UNITS IN VERMETIDAE

The generic and subgeneric names that have been, with some plausibility, applied to members of the family Vermetidae are arranged here in alphabetical order (except for the type genus, *Vermetus*, which is considered first), with references, statement of type species, and discussion of any nomenclatural problems involved. Names available within the family are in bold face type.

Vermetus Daudin, 1800 : 34.

Type species (absolute tautonymy) : *V. adansonii* Daudin, 1800 [based on " Le Vermet " of Adanson, 1757].

The status of this name is somewhat equivocal and will remain so unless it is placed on the Official List of Generic Names by the International Commission on Zoological Nomenclature. Some authors have tried to avoid the difficulties implicit in Daudin's proposal by crediting the name to Cuvier, 1800, but his usage is as an absolute *nomen nudum*, without description or mention of any species. Daudin cited six species that had been described by Adanson, but he gave no formal bibliographic reference to Adanson's publication. On this ground one could justifiably disregard *Vermetus* Daudin and credit the name to the next author who fulfilled the requirements of publication. A substantial barrier stands in the way of this, however, for Daudin at the same time described, in an acceptable manner, four new species that he assigned to *Vermetus*. Although he cited the group as belonging in Gastropoda, every one of his four new species, as the illustrations show, are tubicolous annelids. Therefore, if *Vermetus* as a name cannot be tied to one of the cited Adanson species (all but one of which are molluscan), the name must be transferred to the Annelida, where it would either fall as a synonym or jeopardize some later-established name. In the interests of stability, it seems wisest to be a little lenient, by interpreting Daudin's obvious intention as having been fulfilled. Following is an exact transcription of Daudin's proposal:

"Genre Vermet. Vermetus. Adanson
Vermicularia. Lamarck.

"Caractère générique. Coquille tubulée, tortillée en spirale irrégulière, ordinairement adhérente, et garnie d'une ouverture orbiculaire et operculée.

"Ce genre déja formé par Adanson dans son histoire des coquilles du Sénégal, et confondu par les autres naturalistes et par Bruguière même avec les Serpules, est formé par un gastéropode voisin de celui des planorbes par ses deux tentacules en languette, munis d'un oeil à leur base extérieure; mais il en diffère essentiellement par sa bouche prolongée en une trompe cylindrique garnie de plusieurs rangées de dents crochues, et de plus par un opercule rond très-mince qu'il peut retirer avec lui dans l'intérieur de son tube. Il reste toujours dans la même place, parce que le tube qu'il habite est attaché sur les rochers et sur des coquilles.

"Adanson a décrit les six espèces suivantes.

1. Vermet d'Adanson.	*Vermetus Adansonii.* *Serpula lumbricalis* Linn.
2. Vermet musier.	*Vermetus arenarius.* *Serpula arenaria* Linn.
3. Vermet Datin.	*Vermetus afer.* *Serpula afra* Gm.
4. Vermet Dofan.	*Vermetus Goreensis.* *Serpula Goreensis* Gm.
5. Vermet Lispe.	*Vermetus glomeratus.* *Serpula glomerata* Linn.
6. Vermet Jélin.	*Vermetus intestinalis* *Serpula intestinalis* Gm."

Examining the work by Adanson that Daudin obviously meant—the *Histoire naturelle de Sénégal, Coquillages* (which, being published in 1757, does not itself qualify as a source of generic names)—one finds on page 160 the description of "Le Vermet".

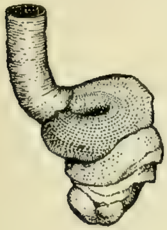
This is the only form so termed by Adanson, although his other five species were described in close association with it and evidently were considered to belong in the same group. I believe that one may interpret Daudin's statement, "Vermet d'Adanson. *Vermetus adansonii*" as fixing the type of *Vermetus* by absolute tautonymy under the current definition of that term in the International Code. The first subsequent designation of the type of *Vermetus* is by Gray (1847), who selected *Serpula lumbricalis* Linné. This would make *Vermetus* an objective synonym of *Vermicularia* Lamarck, 1799. [One may remark that Daudin's citation of Lamarck's species as a synonym perpetuated a common confusion of early authors.] Acceptance of absolute tautonymy as the mode of type fixation for *Vermetus* seems to be the only possibility for retaining the name in its accustomed sense.

Aletes Carpenter, 1857*a* : 226 [not *Aletes* Carpenter, 1857*c* : 301].

Type species (monotypy) : *A. squamigerus* Carpenter, 1857.

Carpenter included the name *Aletes*, as a new subgenus of *Siphonium*, in two manuscripts on which he was working. By the fortunes of publication, the one that carried only a partial diagnosis appeared first, and the only species cited by name therein was of a form described as new that he himself later recognized (Carpenter, 1864 : 654) not to be congeneric with the species he had used as basis for his subgeneric description, *Vermetus centiquadrus* Valenciennes. The latter is, in fact, the only species discussed by Carpenter that fits his diagnosis, "*Operculo parvum concavo, multispirali, fere ut in* Turritella *formato*", and it was selected as type of *Aletes* by Clessin in 1902. My earlier attempt (Keen, 1958 : 297), to preserve Carpenter's intended usage by using the signature dates of what seemed to be an earlier private edition issued by Carpenter, now seems ill-advised in view of evidence published by Iredale (1916 : 36) that I had not considered sufficiently. As Iredale demonstrated, Carpenter's edition was instead a later re-issue of the British Museum official publication. These signature dates must therefore be regarded as dates of printing rather than dates of release to the public.

The species *A. squamigerus* is non-operculate, and the shell is so similar in form to that of the type of *Serpulorbis* that we can hardly maintain *Aletes* as a morphologically distinct group with it as type. The only way the generic name could be salvaged for use in the West American fauna would be to petition the International Commission on Zoological Nomenclature that *Aletes* be made a *nomen conservandum*, with *A. centiquadrus* as type. One might argue that Carpenter's mis-allocation of his new species to *Aletes*, which he himself later rejected, might constitute a form of misidentification, and one could thus ask to have *Aletes* preserved. However, one would be on rather insecure ground in trying to prove that this is the accustomed sense in which the generic name has been used, for a census of the literature would be most apt to show that the combination "*Aletes squamigerus*" has appeared more frequently than the combination "*A. centiquadrus*". Also, such action is a matter that would require several years of time. At present, it seems better to let *Aletes* lapse into synonymy and to place *Vermetus centiquadrus* in *Vermetus*, *s. l.*, until material is available for a careful study of soft parts and nuclear whorls, neither of which have been described. The one operculum illustrated here (figs. 2–3) is distinctive, and if additional material proves similar, a separate generic category for this species would surely seem justified.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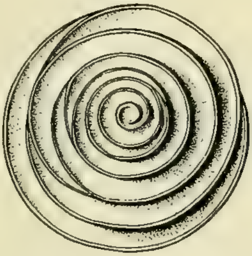
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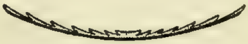
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FIG. 1. *Vermetus centiquadrus.* Stanford Univ. specimen, West Mexico. ×½.
FIG. 2. Same, operculum, full view. ×9.
FIG. 3. Section of operculum to show laminae. ×9.

Anguinella Conrad, 1845–46 in 1838–61 : 77. [Not *Anguinella* Van Beneden, 1845.]
Type species (monotypy) : *Serpula virginica* Conrad.

Bivonia Gray, 1847 : 156. [Not *Bivonia* Cocco, 1832.]
Type species (original designation) : *Vermetus glomeratus* Bivona-Bernardi, 1832.

Cladopoda Gray, 1850 : 83.
Type species (subsequent designation, Tryon, 1886) : *C. grandis* Gray, 1850 [based on " *Vermetus arenarius* " of Quoy & Gaimard, not Linné].

Cryptobia Deshayes, 1863 : 65. [Not *Cryptobia* Leidy, 1846. Probably not a mollusc.]

Dendropoma Mörch, 1861 : 153.
Type species (here designated) : *Siphonium* (*D.*) *lituella* Mörch, 1861.

Dofania Mörch, 1860*a* : 34.
Type species (subsequent designation, Bucquoy, Dautzenberg & Dollfus, 1884) : Le Dofan Adanson = *Serpula goreensis* Gmelin, 1791.

Adanson's type specimen of Le Dofan seems no longer to be discoverable, according to Fischer-Piette (1942 : 264). As the type figure does not permit of specific determination, the generic name is at present unusable.

Elliptovermetus Cossmann & Peyrot, 1922 : 69.
Type species (original designation) : *Vermetus breigneti* Cossmann & Peyrot ; Aquitanian (Upper Oligocene) of France.

Hatina Gray, 1847 : 156.
Type species (monotypy) : " *Verm. inoperculatus* " [apparently an error for *Vermetus inopertus* Rüppel & Leuckart, 1830–31].

This is probably a synonym of *Serpulorbis*, but uncertainty as to the name of the type species suggests that it be classed as a *genus dubium*.

Macrophragma Carpenter, 1857*b* : 308.
Type species (absolute tautonymy) : *Petaloconchus macrophragma* Carpenter, 1857.
The name was only tentatively proposed by Carpenter but was accepted by Mörch in 1861, so that it is available for use.

Magilina Vélain, 1877 : 105.
Type species (monotypy) : *M. serpuliformis* Vélain.

Novastoa Finlay, 1927 : 386.
Type species (original designation) : *Siphonium lamellosum* Hutton, 1873.

Petaloconchus Lea, 1843 : 233.
Type species (monotypy) : *P. sculpturatus* Lea ; Miocene of Virginia.

Polyphragma Vaillant, 1871 : 189. [Not *Polyphragma* Quatrefages, 1866.]
Type species (monotypy) : *Vermetus varians* Orbigny, 1841.

Scolissedium " Rein. " Verany, 1846 : 15. Evidently an erroneous spelling of *Scolixedion*, q. v.

Scolixedion Renier, 1807, of authors. Invalidated by the International Commission (I.C.Z.N., 1957), and placed on the " Official Index of Rejected Generic Names " (I.C.Z.N., 1958).

Serpuloides Gray, 1850 : 83. [Not *Serpuloides* Murchison, 1839.]
Type species not selected.

Serpulorbis Sassi, 1827 [also recorded as Sasso] : 482.
Type species (monotypy) : *S. polyphragma* Sassi = *Serpula arenaria* Linné, 1758.
The generic name has been misspelled as *Serpulopsis* by some authors.

Siphonium Gray, 1847, of authors [not *Siphonium* Link, 1807] = *Vermicularia.*

Siphonium " Browne " of Mörch, 1859 : 348, 353 [not of Link, 1807] = *Dendropoma.*

Spiroglyphus Daudin, 1800 : 39.
Type species (subsequent designation, Mörch, 1861) : *S. annulatus* Daudin.
Daudin described the shells of two species, without being sure whether they were worms or molluscs. He cited the type locality of *S. annulatus* as the Indian Ocean, on Fissurellas and Patellas. His principal distinction for the genus was that it corrodes a channel for itself. His type figure is of an irregularly coiled shell on what looks to be a Caribbean *Diodora*, which has led some authors to reinterpret the type locality. There are some tube-dwelling worms that resemble his figure, although they may not truly corrode a channel as one group of vermetid gastropods do.

Dr. Olga Hartman, specialist on Annelida, to whom a photograph of Daudin's figure was submitted, could not positively identify the form either as an annelid or as not an annelid. I feel the same hesitation about saying definitely whether or not the figure represents a vermetid gastropod. Hence, we would need some objective basis other than the figure before we could accept the name *Spiroglyphus* as valid in Vermetidae. Rediscovery of Daudin's type specimen might solve the problem, but inquiries in France have brought no clues. Dr. E. Fischer-Piette, in fact, reported that he would not even know where to start a search. Another possibility would be the selection of a neotype, a course acceptable under the International Rules and one which I had planned to adopt, but I have found no specimen in the collections available (including that storehouse of malacological treasures, the British Museum of Natural History) that would satisfy the necessary requirements. The name *Spiroglyphus* has been widely used in the Gastropoda—true—but it has also been used by some palaeontologists, probably incorrectly, for the annelid group of *Tubulostium* Stoliczka, 1868, or *Rotularia* Defrance, 1827. For the present, therefore, it seems advisable to set it aside as a *genus dubium* until such time as it can be given unequivocal status with a type species based on a recognizable specimen, either by rediscovery of Daudin's material or by finding an acceptable neotype—both possibilities now seeming rather unlikely.

Tetranemia Mörch, 1859 : 353.

Type species (monotypy) : *Serpulus* (*T.*) *dentiferus* (Lamarck) of Quoy & Gaimard (not of Lamarck) = *Thylacodes* (*T.*) *longifilis* Mörch, 1862.

Thylacodes Agassiz, 1846 : 370, 381. *Nomen nudum.*

Thylacodes Mörch, 1862 : 64 (*ex* Guettard, 1774, non-binomial).

Type species (here designated) : *Serpulorbis polyphragma* Sassi, 1827 = *Serpula arenaria* Linné, 1758.

Thylacodus Mörch, 1860*b* : 77 (July).

Type species (here designated) : *Vermetus contortus* (Carpenter) = *Bivonia contorta* Carpenter, 1857.

Other species included by Mörch : *V.subcancellatus* Bivona-Bernardi, *V. conicus* Dillwyn, and *V. contortus* var. *indentatus* Carpenter.

Thylaeodus Mörch, 1860*a* : 48 (January).

Type species (here designated) : *Vermetus contortus* (Carpenter) = *Bivonia contorta* Carpenter, 1857.

Mörch proposed the name in a postscript to his first paper, as follows : " Enfin, je proposerai le nom de *Thylaeodus* pour les Vermets sans plis." As it stands, this seems too vague to be a valid proposal, but careful reading of the paper, especially page 39, shows that he would include these species in the category of vermetids without folds : *V. contortus* and its variety, *V. albidus* Carpenter ; *V. subcancellatus* Bivona-Bernardi ; and *V. carinatus* Quoy & Gaimard. One may suspect that the spelling "*Thylaeodus*" was a printer's error, for in the subsequent paper, where more formal treatment was given, the spelling was consistently "*Thylacodus*". However, under the International Rules, the original spelling must be accepted unless evidence in the paper itself demonstrates an error. Mörch having given no clue as to derivation, we must adopt *Thylaeodus* as the valid spelling. In a way this is advantageous, for thus we avoid the confusion of *Thylacodus* with *Thylacodes*, names used by Mörch in different senses.

Veristoa Iredale, 1937 : 254.
Type species (original designation) : *V. howensis* Iredale.

Vermiculus Mörch, 1859 : 348 (*ex* Lister). [Not *Vermiculus* DaCosta, 1776 nor Linck, 1783.]
As of Mörch, this is a synonym of *Vermicularia*. The name is a pre-Linnean term, used non-binomially by later authors for a mélange of forms. The earliest such use is by DaCosta for three unnamed species, one of which is a *Serpulorbis*. It would seem to serve no useful purpose and should be placed on the Official Index of Rejected Generic Names.

Vermitoma Kuroda, 1928 : 40.
Type species (monotypy) : *V. luchuana* Kuroda (*ex* Hirase MS.). [Description in Japanese.]

C. REVISED CLASSIFICATION OF THE VERMETIDAE

Generic synonymies, as now understood, are given below, with notes on shell morphology and lists of the species that, with some confidence, one may assign to each group. Citations are, in the main, only to author and date but full references for many species are given in Section D.

Family VERMETIDAE Gray, 1828

Sessile gastropods with shells more or less firmly attached throughout life to rock or to other shells ; coiling irregular to disjunct (lax) ; axis of coiling of nuclear whorls at a right angle to that of later whorls ; operculum chitinous, spiral, with a tendency toward external laminae.

Genus ***VERMETUS*** Daudin, 1800

? *Dofania* Mörch, 1860.

Mainly solitary or in small clusters, coiling usually irregular ; columellar wall smooth, without laminae ; nuclear whorls two, globose to elongate ; operculum thin, spiral, one-half or less the diameter of the aperture.

Subgenus ***VERMETUS***, *s. l.*

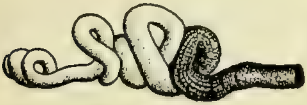
Into this category must be grouped all the otherwise unassignable species—those described on the basis of incomplete shells, those of unknown provenance, and those not yet studied in adequate detail. The major part of some 250 named forms, fossil and living, fall herein.

Subgenus *VERMETUS*, s. s.

(Text-figs. 4–7)

Coiling irregular but shell mostly well attached; without feeding-tube scars; colour, brown; operculum small, less than half the diameter of the aperture, consisting of a concave disc with a spiral lamina of one to two turns (Text-figs. 6–7); nepionic shell of two subglobular whorls (Text-fig. 5).

Until recent years (Fischer-Piette, 1942), the type material of *V. adansonii* was lost to science. In the meantime, authors had misdetermined the species and confused it with a *Petaloconchus* (*Macrophragma*) from other parts of West Africa. That the type species of *Vermetus* does not show any internal spiral laminae is confirmed both by the original material (Fischer-Piette, 1942, pl. 9, figs. 3–5) and by topotype specimens.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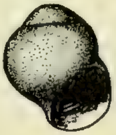
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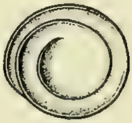
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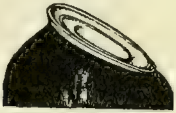
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FIG. 4. *Vermetus adansonii*, lectotype, after Fischer. ×0·75.
FIG. 5. Nuclear whorls of *V. adansonii*, topotype. ×30.
FIG. 6. Same, operculum full view. ×35.
FIG. 7. Oblique view of operculum as seen on dried animal. ×35.

Assignable species:

V. (*V.*) ***adansonii*** Daudin, 1800 [type species]. West Africa, especially Sénégal.
V. (*V.*) *afer* (Gmelin, 1791). West Africa, especially Sénégal.
V. (*V.*) *triqueter* (Bivona-Bernardi, 1832). Mediterranean.

Subgenus *THYLAEODUS* Mörch, 1860*a* (January)

(Text-figs. 8–11)

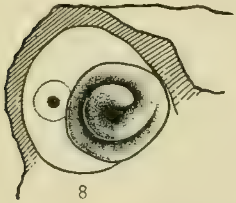
Bivonia of authors, not of Gray, 1847; *Thylacodus* Mörch, 1860*b* (July).

Buff to brown shells of moderate or small diameter, with strongly cancellate to beaded sculpture; feeding-tube scars (abandoned remnants of former vertical tubes) present on most specimens; operculum one-half to three-fourths the diameter of the aperture, with a spiral lamina of chitin that rises free from the disc.

These shells have been grouped by many authors, following Carpenter, in the genus *Bivonia*, but this is untenable on two counts: the name is preoccupied and the type species differs in several significant features. Though resembling *Petaloconchus* externally, this group consistently lacks the internal spiral laminae and thus is closer to *Vermetus*, s. s.

Assignable species :

V. (*T.*) *contortus* (Carpenter, 1857) [type species]. Tropical West America.
V. (*T.*) *indentatus* (Carpenter, 1857). Tropical West America.
V. (*T.*) *?quoyi* (H. & A. Adams, 1854). Indo-Pacific.
V. (*T.*) *semisurrectus* Bivona-Bernardi, 1832. Mediterranean.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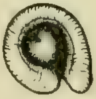
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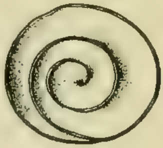
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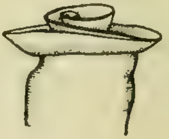
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FIG. 8. *V.* (*Thylaeodus*) *contortus*, showing operculum in place in a broken aperture. Topolobampo, West Mexico. × 12.

FIG. 9. *V.* (*T.*) *contortus*, apex of nuclear whorls, as seen from attached side, showing also the first subsequent whorl. × 12.

FIG. 10. *V.* (*T.*) *indentatus*, operculum, full view. Guaymas, West Mexico. × 17.

FIG. 11. Same specimen, side view of operculum. × 17.

Genus ***SERPULORBIS*** Sassi, 1827

Lemintina of authors (not of Risso, 1826) ; *Anguinella* Conrad, 1846, preoccupied ; *Hatina* Gray, 1847 ; *Serpuloides* Gray, 1850, preoccupied ; *Aletes* Carpenter, 1857*a* ; *Tetranemia* Morch, 1859 ; *Thylacodes* Mörch, 1862*b*.

Shells among the largest of the family, the coiling of roughly concentric loops, especially in the early whorls, the later coiling in colonial forms being densely contorted, lax, or hardly apparent. Scars of broken feeding tubes apparent on most specimens. Colour of shells ranging from dark brown to pure white. Nuclear whorls lighter in colour than the rest of the shell, of two to four whorls, globose-conic rather than cylindrical. Operculum wanting.

Subgenus ***SERPULORBIS***, *s. s.*

(Text-figs. 12–14)

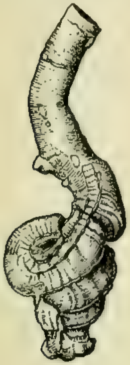
Colonial forms, in the main, with tubes that are concentrically looped in the young to weakly contorted in the adult ; sculpture of spiral lines variously intersected to form nodes or scales.

Assignable species :

S. (*S.*) *arenaria* (Linné, 1758). Mediterranean. (Synonyms : *S. polyphragma* Sassi, 1827 [type species] ; *Vermetus gigas* Bivona-Bernardi, 1832.)
S. (*S.*) *decussatus* (Gmelin) [*Serpula*]. Caribbean.
S. (*S.*) *cruciformis* (Mörch, 1862) [*Thylacodes*]. West Mexico.
S. (*S.*) *masier* (Deshayes, 1843) [*Vermetus*]. West Africa.
S. (*S.*) *medusae* (Pilsbry, 1891) [*Thylacodes*]. Japan.

S. (S.) *novaehollandiae* (Chenu, 1843, *ex* Rousseau MS) [*Vermetus*]. ?Australia.
S. (S.) *sipho* (Lamarck, 1818) [*Serpula*]. Indo-Pacific.
S. (S.) *squamigerus* (Carpenter, 1857) [*Aletes*]. California.
S. (S.) *validus* Kuroda & Habe, 1952. Japan.

This group seems to have appeared earliest in time of the vermetids, as early at least as Eocene time : for example—among others—S. *morchi* and S. *cancellatus* Deshayes, 1861, from the lower and middle Eocene of Europe, and S. *chavani* Harris & Palmer, 1946, from the upper Eocene of south-eastern United States. Some Upper Cretaceous forms have a pattern of coiling that seems *Serpulorbis*-like—as in S. *lamellosus* (Stoliczka, 1868), from India—although the preservation is not complete enough to provide indisputable evidence that these are gastropods and not tubicolous annelids.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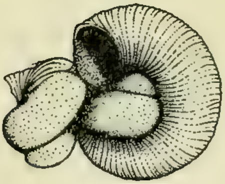
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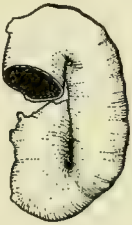
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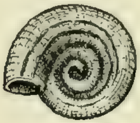
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FIG. 12. *Serpulorbis arenarius* (Linné), after Monterosato. Mediterranean. × ½.
FIG. 13. S. *arenarius*, nuclear whorls. Sicily (Stanford Univ. collection). × 22.
FIG. 14. S. *polyphragma*, shell, after Priolo. × ½.
FIG. 15. S. (*Cladopoda*) *grandis*, shell, after Quoy & Gaimard, somewhat modified from specimens. Indo-Pacific. × ½.

Subgenus ***CLADOPODA*** Gray, 1850

(Text-fig. 15)

Coiling planorboid throughout life (rarely lax) ; shells mostly solitary rather than colonial, large in diameter, with the entire coil in contact with the substrate ; colour of shell ivory white to blackish brown ; sculpture of longitudinal threads that are but weakly intersected by transverse sculpture.

Assignable species :

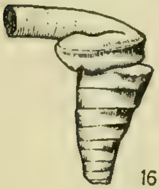
S. (C.) *colubrinus* (Röding, 1798) [*Serpula*]. Indo-Pacific area. (Synonym : *V. ater* Chenu, 1844.)
S. (C.) *grandis* (Gray, 1850) [type species : as *Cladopoda*]. Indo-Pacific.
S. (C.) *imbricatus* (Dunker, 1860) [*Vermetus*]. Japan.
S. (C.) *margaritaceus* (Chenu, 1844, *ex* Rousseau MS.) [*Vermetus*]. Probably West Mexico. (Synonym : *V. margaritarum* Valenciennes, 1846.)

Genus ***TRIPSYCHA***, new genus

(Text-figs. 16–20)

Type species : *Vermetus tripsycha* Pilsbry & Lowe, 1932. West Mexico.

White shells of moderate size, with the early whorls firmly attached and coiling as in *Serpulorbis* ; medial and later whorls mostly unattached and coiling in hollow cone form, somewhat as in *Petaloconchus*, *s.s.* ; last whorl lax and uncoiled. Operculum slightly concave, with an appressed spiral lamina of several volutions. Nuclear whorls unusually large, with several turns, rather more elongate than in most vermetids except some *Petaloconchus* (*Macrophragma*). Mainly solitary shells, but when crowded they may form a radiating cluster of tubes, due to the tendency of each individual to grow away from any nearby competitor.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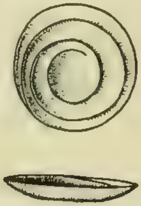
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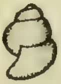
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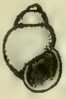
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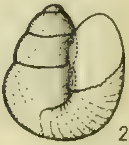
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Fig. 16. *Tripsycha tripsycha*, holotype, after Pilsbry & Lowe ; Guyamas, Mexico. × ½.
Fig. 17. *T. tripsycha*, operculum, full and side views. Stanford Univ. collection. Guaymas. × 5.
Fig. 18. Same, nuclear whorls, side view ; from brood capsule. × 15.
Fig. 19. Same specimen as Fig. 18, apertural view. × 15.
Fig. 20. Nuclear whorls, after attachment to substrate. Stanford Univ. collection, Guaymas. × 17.

The name of the subgenus is that of the type species, as this seems to be a very suitable noun coined by Pilsbry & Lowe from the Greek words *tri* and *psyche* and evidently intended to convey the meaning, " of three minds ", in reference to the three modes of coiling during the life of the individual.

Assignable species :

T. tripsycha (Pilsbry & Lowe, 1932). West Mexico.

Genus ***PETALOCONCHUS*** Lea, 1843

Petaloconcha, unjustified emendation by Cossman, 1912.

Coils forming a hollow cylinder, at least in the young ; medial whorls with a more or less complex internal structure of spiral laminae projecting from the columellar wall.

Subgenus ***PETALOCONCHUS***, *s. s.*

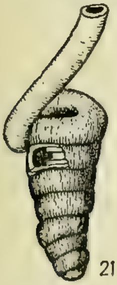
(Text-fig. 21)

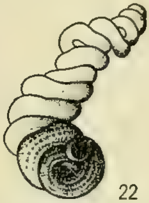
Last whorl lax or unwound, earlier whorls forming a symmetrical hollow cone. Nuclear whorls and operculum unknown. Sculpture, when present, evenly cancellate.

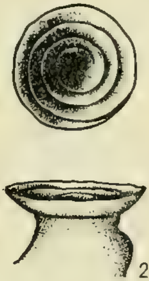
The type species was described from the Miocene of the eastern United States. A few closely related species have since been described, all in the Middle Tertiary of the Caribbean area. The subgenus in the strict sense is not recorded elsewhere.

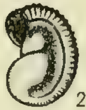
Assignable species :

P. (*P.*) *sculpturatus* Lea, 1843. Miocene, Virginia [type species : holotype refigured, Gardner, 1947, pl. 55, fig. 21]. (Synonym : *P. domingensis* Sowerby, 1849.)









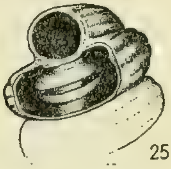


FIG. 21. *Petaloconchus sculpturatus*. Specimen, Stanford Univ. collection, from the Miocene of Trinidad, with internal laminae showing in the broken section of one coil. ×½.

FIG. 22. *P.* (*Macrophragma*) *macrophragma*, sketch of lectotype, to illustrate coiling. Mazatlán, Mexico. ×2. B.M. (N.H.) Reg. No. 57.6.4.1500.

FIG. 23. *P.* (*M.*) *macrophragma*. Operculum. Stanford Univ. collection. ×13.

FIG. 24. Same, nuclear whorls. West Mexico. ×12·5.

FIG. 25. Detail of columellar laminae. Stanford Univ. collection, Oaxaca, Mexico. ×6.

Subgenus ***MACROPHRAGMA*** Carpenter, 1857

(Text-figs. 22–25)

Polyphragma Vaillant, 1871 [not Quatrefages, 1866] ; *Petaloconchus*, *s. s.* of authors.

Coiling regular, especially in the early whorls, described by Carpenter as "like a *Turritella* squeezed sideways". Sculpture cancellate, but with the longitudinal ribs tending to be predominant and sub-carinate.

Nuclear whorls two to four, ivory white to waxy yellow, conic to cylindrical. Adult shell medium to dark brown in colour. Operculum concave, with an upstanding spiral lamella of one or two volutions, diameter less than that of the aperture, resembling that of *Vermetus* (*Thylaeodus*) in form.

The shells are either solitary or colonial and are mostly smaller in size than in other vermetid groups except *Vermetus* (*Thylaeodus*), which they closely resemble except for more regular coiling and the internal spiral lamellae. Scars of broken feeding tubes are common and may recur at regular intervals along the coil.

Assignable species :

P. (*M.*) *cereus* Carpenter, 1857. Philippines.

P. (*M.*) *cochlidium* Carpenter, 1857. Australia.

P. (M.) *complicatus* Dall, 1908. Panama Bay.

P. (*M.*) *flavescens* Carpenter, 1857. "Sicily" (evidently in error). Probably from West Mexico.

P. (*M.*) *floridanus* Olsson & Harbison, 1953. Florida, Pliocene to Recent.

P. (*M.*) *glomeratus* (Linné, 1758) [*Serpula*]. Mediterranean. (Synonym : *Vermetus subcancellatus* Bivona-Bernardi, 1832.)

P. (*M.*) *innumerabilis* Pilsbry & Olsson, 1935. Tropical West America.

P. (*M.*) *interliratus* Stearns, 1893. Cape Verde, West Africa.

P. (*M.*) *macrophragma* Carpenter, 1857 [type species]. West Mexico.

P. (*M.*) *mcgintyi* (Olsson & Harbison, 1953) [*Lemintina*?]. Florida, Pliocene to Recent.

P. (*M.*) *montereyensis* Dall, 1919. California.

P. (*M.*) *nerinaeoides* Carpenter, 1857. Australia.

P. (*M.*) *renisectus* Carpenter, 1857. Indo-Pacific.

P. (*M.*) *tokyoensis* Pilsbry, 1895. Japan.

P. (*M.*) *varians* (Orbigny, 1841) [*Vermetus*]. Caribbean.

Genus ***DENDROPOMA*** Mörch, 1861

Spiroglyphus of authors, probably not of Daudin, 1800 ; *Stoa* of authors, not of De Serres, 1846 (annelid) ; *Bivonia* Gray, 1847 [not Cocco, 1832] ; *Siphonium* Mörch, 1859 [not Link, 1807] ; *Magilina* Vélain, 1877 (?) ; *Vermitoma* Kuroda, 1928 ; *Veristoa* Iredale, 1937.

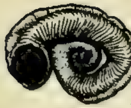
Solitary to colonial forms, corroding a trench in the substrate, in which the lower part of each volution is embedded ; coiling planorboid in early whorls, becoming looser in later whorls, with a tendency toward right-angled turns. Colour of adult mostly white, variously stained with dark brown, especially within. Sculpture of lamellar growth-striae that may or may not be intersected by longitudinal lines, sinuous and rising toward a crest near the outer edge of the whorl in most species. Nuclear whorls two, dark brown in colour, inflated, smooth to malleated or axially ribbed, the apertural lip pointed or claw-like in some species. Operculum well developed, as large in diameter as the aperture, its inside surface having a distinct central attachment-scar that is somewhat button-like, its outside composed of chitinous plates in a spiral arrangement, either compactly welded to form a smooth surface or variously agglutinated with foreign materials.

Subgenus ***DENDROPOMA***, *s. s.*

(Text-figs. 26–29)

Mainly solitary forms, minute to large, burrowing in other shells or in coral, rarely attached to rock. Operculum concave in large forms, flattened in smaller ones, buff-brown to mahogany red in colour. Sculpture varying from weak transverse threads to heavy longitudinal rows of scales.

The largest specimen of *D. maximum* seen (at the British Museum [Nat. Hist.]), had attained a length of over 18 inches. This is very exceptional. A diameter of 22 mm. is not uncommon in the larger forms, however. *D. maximum* is the form cited by Yonge and others from the Great Barrier Reef under the incorrect identification of *Vermetus novae-hollandiae*, the latter being a *Serpulorbis*.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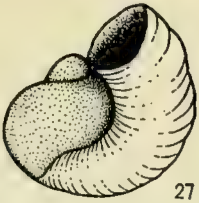
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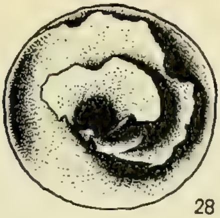
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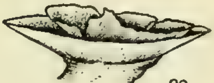
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FIG. 26. *Dendropoma lituella*, sketch of lectotype, to illustrate manner of coiling. California. ×3. B.M. (N.H.) Reg. No. 195917.

FIG. 27. *D. lituella*, nuclear whorls. Stanford Univ. collection, southern California. ×25.

FIG. 28. Same, operculum, full view of a specimen with the membranous laminar surface exceptionally well preserved. ×10.

FIG. 29. Side view of same specimen.

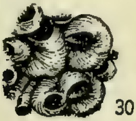
Assignable species :

D. (*D.*) *andamanicum* (Prashad & Rao, 1933) [*Vermetus*]. Indian Ocean.
D. (*D.*) *corrodens* (Orbigny, 1842) [*Vermetus*]. Caribbean.
D. (*D.*) *leucozonias* (Mörch, 1861) [*Siphonium*]. West Africa.
D. (*D.*) *lituella* (Mörch, 1861) [type species : as *Siphonium*]. California.
D. (*D.*) *luchuanum* (Kuroda, 1928) [*Vermitoma*]. Japan.
D. (*D.*) *marchadi* Keen & Morton, 1960. West Africa.
D. (*D.*) *maximum* (Sowerby, 1825) [*Serpula*]. East Indies. [Lectotype in B.M. (N.H.).]
D. (*D.*) *nebulosum* (Dillwyn, 1817) [*Serpula*]. Caribbean.
D. (*D.*) *planorbis* (Dunker, 1860) [*Vermetus*]. Japan.
D. (*D.*) *rastrum* (Mörch, 1861) [*Vermiculus*]. California.

Subgenus ***NOVASTOA*** Finlay, 1927

(Text-figs. 30–33)

Colonial forms, usually encrusting rocks in honeycomb-like sheets. Nuclear whorls as in *Dendropoma*, *s. s.*, later whorls in tight, angulate coils spiralling upward from substrate. Operculum bright reddish brown, flattened to convex, the inner central mamilla conspicuous, the inner margin polished, the outer surface scaly.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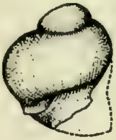
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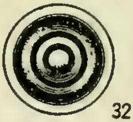
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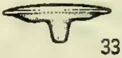
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FIG. 30. *D.* (*Novastoa*) *lamellosum*. Detail of part of a colony. Stanford Univ. collection, from New Zealand. ×1·5.

FIG. 31. Nuclear whorls, redrawn, from Morton, 1951. ×25.

FIG. 32. Operculum, inner surface, showing the polished rim. After Morton. ×7.

FIG. 33. Same, side view, showing the large mamilla. ×7.

This group may be only situs forms, not a true genetic unit, for specimens in the dense clumps may be, to the eye, indistinguishable from solitary specimens as to operculum, nuclear whorls, and sculpture. Yet, when one compares such clumps from various geographic areas with the type species of *Novastoa*, one finds such a similarity of appearance as to suggest the usefulness of a subgeneric group name.

Assignable species :

D. (*N.*) *corallinaceum* (Tomlin, 1939) [*Vermetus*]. South Africa.

D. (*N.*) *ghanaense* Keen & Morton, 1960. West Africa.

D. (*N.*) *irregulare* (Orbigny, 1842) [*Vermetus*]. Caribbean.

D. (*N.*) *lamellosum* (Hutton, 1873) [type species : as *Siphonium*]. New Zealand.

D. (*N.*) *petraeum* (Monterosato, 1884) [*Bivonia*]. Mediterranean. (Synonym : *Vermetus glomeratus* Bivona-Bernardi, 1832 [not Linné, 1758].)

D. (*N.*) *tholia* Keen & Morton, 1960. East Africa.

Subgenus ***ELLIPTOVERMETUS*** Cossmann & Peyrot, 1922

The tube of the type species is ovate in cross-section, deeply immersed in a coral and showing lamellar growth-striae fluted by longitudinal ribs. Known only in beds of Aquitanian age (U. Oligocene) of France.

Assignable species :

D. (*E.*) *breigneti* (Cossman & Peyrot, 1922) [type species : as *Vermetus*]. French Aquitanian.

D. NOTES ON TYPE AND OTHER SPECIMENS

Vermetus adansonii Daudin, 1800

(Text-figs. 4–7)

V. adansonii Daudin, 1800 : 35.

Topotype material supplied by M. I. Marche-Marchad, of the Station de Biologie Marine de l'Institut Français d'Afrique Noire, provides at long last a firm basis for reappraisal of this type species. Concerning the locality M. Marche-Marchad says, (letter dated 20th December, 1954) : " Les exemplaires que je vous ai envoyés sont probablement des topotypes au sens le plus étroit du terme. En effet l'Ile aux Serpents = l'Ile de la Madeleine d'Adanson. C'est un petit îlot rocheux, très battu, situé à environ 2 milles à l'ouest du Cap Vert. Les 'bassins où l'eau de la mer est tranquille' et 'creusés naturellement dans le roc' (Adanson) n'abondent pas ; il n'y y en qu'un, c'est le 'lagon' d'où proviennent nos Vermets. Ce lagon n'a pas plus de 200 m. de periphérie et si ces mollusques ne viennent pas du rocher même ou Adanson les a observés—ce qui est probable—ils n'en sont certainement pas très éloignés! "

Fischer-Piette (1942) has figured Adanson's actual type material, rediscovered during the early part of World War II. The coiling of the shell is loose and rather irregular, and the medial whorls do not exhibit within any sign of the spiral laminae attributed to the species by Mörch. The present topotype specimens supply needed details as to the nuclear whorls (Text-fig. 5) and the operculum (Text-figs. 6–7).

A lectotype for *Vermetus adansonii* Daudin is here selected, the specimen of fig. 4, illustrated by Fischer-Piette on his pl. 9, fig. 3. It is in the collection of the Muséum National d'Histoire naturelle de Paris.

One concludes that the " crust " from Gaboon, equatorial Africa, identified by Mörch (1861 : 337) as *Vermetus adansonii*—which formed the concept of the species for many later authors—was not a true *Vermetus*. The latter seem to be rather more solitary forms than Mörch's description implies. His may have been the *Petaloconchus interliratus* Stearns, 1893 (a species based only on a type locality [Porte Grande, St. Vincent, Cape Verde, West Africa] and a vague description [" an elevated, threadlike ridge following the coiling spirally "]). Stearns' syntype material, cited by number (U.S. Nat. Mus. No. 125,378), is a tight colony of *Petaloconchus* (*Macrophragma*) with internal laminae well developed.

Vermetus (Vermetus) afer (Gmelin, 1791)

Serpula afer Gmelin, 1791 : 3745.

Fischer (1942 : 264) in refiguring Adanson's " Le Datin " suggested that it may be composite. Topotype specimens, however, taken by M. Marche-Marchad with the *V. adansonii*, match Fischer-Piette's figures well and seem to constitute a good species differing from *V. adansonii* by having rather regular planorboid coiling. This seems also to be more solitary. As a lectotype the specimen figured by Fischer-Piette on pl. 9, fig. 6 is here selected. It is in the Muséum National d'Histoire naturelle de Paris. The operculum of the topotype specimens is like that of *V. adansonii*.

Vermetus (Thylaeodus) contortus (Carpenter, 1857)

(Pl. 55, fig. 3)

Bivonia contorta Carpenter, 1857*c* : 305.

Lectotype (here selected) : B.M. (N.H.) Reg. No. 57.6.4.1490. Mazatlán, Mexico.

Carpenter's best specimen was broken and his others considered to be young, which has led to misinterpretation of the adult form by later authors, including myself (Keen, 1958 : 298, fig. 200—a figure actually of an enigmatic *Serpulorbis*). However, Tryon (1886, pl. 49, fig. 27) seems to have figured it correctly. New material from near Mazatlán, collected by Mr. James McLean in December, 1959, affords opportunity to study a growth series taken alive. The adults are small (diameter of aperture about 2 to 3 mm.), the coiling somewhat less regular than that of the superficially similar *Petaloconchus* (*Macrophragma*) *macrophragma*. The colour is a warm wax-brown, and the sculpture is of longitudinal threads evenly beaded at the intersections of cross-threads, the whorls rounded in section, rarely rendered angulate by the lirae. Internal spiral laminae are completely lacking. A mature coil may be only 15–20 mm. in length. The two nuclear whorls are conic, moderately inflated, and pinkish brown in colour. The operculum has a spiral lamina that stands up from the cup ; the diameter is about half the diameter of the aperture.

This species is here selected as type of *Thylaeodus*. Previous allocation to *Bivonia* is untenable on two counts, as shown above (p. 193). The assignment to *Petaloconchus*—suggested by workers who discount the importance of the internal laminae in classification—although plausible as to form of operculum and nuclear whorls, would seem to broaden the limits of that group unduly. With a new insight as to the morphology of *Vermetus*, we can now suggest that this and a few related species could well form a subgenus under *Vermetus*.

Vermetus (Thylaeodus) indentatus (Carpenter, 1857)

(Plate 55, fig. 4)

Bivonia contorta, var. *indentata* Carpenter, 1857*c* : 307.

Lectotype (here selected) : B.M. (N.H.) Reg. No. 57.6.4.1494. Mazatlán, Mexico.

In the lectotype, the longitudinal sculpture is heavier and less evenly beaded than in *V.* (*T.*) *contortus*. Coiling seems also to be less regular. The lectotype is dark brown in colour. A variant form, which may prove to be a separate species, is pinkish buff, with evenly cancellate sculpture. This species ranges more widely in the Gulf of California than does *V. contortus*.

Serpulorbis (Serpulorbis) arenarius (Linné, 1758)

(Text-figs. 12–13)

Serpula arenaria Linné, 1758 : 787. " Habitat in Indiis."
Serpulorbis polyphragma Sassi, 1827 : 484. Mediterranean.
Vermetus gigas Bivona-Bernardi, 1832 : 5, pl. 2, figs. 1–2. Mediterranean.

Linné's species is now generally considered to be the common large Mediterranean vermetid, better known under the name of *S. gigas*. *S. polyphragma* Sassi, type of *Serpulorbis* (see Text-fig. 14), seems to be only a smooth or unsculptured variant of the species. *S. arenarius* may form dense colonies of contorted tubes. Coiling of the young shell is planorboid. A report by Dr. Ottavio Priolo (1956*a*) gives evidence on the rapidity of growth : the hull of a boat sunk in a Sicilian harbour during World War II, raised in 1956, was covered with large masses of these shells. Specimens of these, sent to Stanford University, measure 13 mm. in diameter at the aperture and would be several inches long if the tubes were not contorted.

Serpulorbis (Serpulorbis) constrictor (Mörch, 1862)

Bivonia constrictor Mörch, 1862*b* : 63. Australia.

? Holotype : B.M. (N.H.) Reg. No. 195919.

Hedley (1913 : 294, pl. 18, fig. 71) figured this species with the statement, " In the British Museum is a single specimen, perhaps the type, but not so labelled . . . " Iredale (1937 : 254) considered that it is the type, which seems plausible.

Serpulorbis (Serpulorbis) eruciformis (Mörch, 1862)

(Pl. 54, fig. 3)

Thylacodes eruciformis Mörch, 1862*b* : 70. "California."

Holotype : B.M. (N.H.) Reg. No. 195915, on a *Crucibulum*. Probable type locality, the Gulf of California.

The type specimen consists of three whorls, with a beaded sculpture pattern. It measures about 30 by 35 mm. in total size.

Serpulorbis (Serpulorbis) squamigerus (Carpenter, 1857)

(Plate 55, fig. 5)

Aletes squamigerus Carpenter, 1857*a* : 226. Santa Barbara, California.

Syntype cluster : B.M. (N.H.) Reg. No. 55.3.14.57 (Nuttall Coll.) [*teste* S. P. Dance, 1959].

Carpenter himself in 1864 referred this to *Serpulorbis*, evidently realizing that it is not congeneric with *V. centiquadrus*. The sculpture varies from extreme scaliness to weak wrinkles, depending upon such factors as rapidity of growth, degree of crowding, etc. The geographic range is from Monterey, California, to southern Baja California. A similar and hitherto unrecognized species of *Dendropoma*, *D. rastrum* (see p. 207), occurs in the same area, distinguishable by the presence of an operculum and by a corroding habit. The two are doubtless confused in most collections.

Serpulorbis (?Cladopoda) oryzata (Mörch, 1862)

(Pl. 54, fig. 1)

Thylacodes ? oryzata Mörch, 1862*b* : 78. "China."

Holotype : B.M. (N.H.) Reg. No. 195912. Probably West Mexico.

Mörch correctly surmised that this shell in the Cuming collection had not come from China but from West Central America. It is a solitary form, with a few closely coiled whorls at first, and then coiling becomes not merely lax but obsolete, for the tube may stretch out in a weak curve for a distance of several inches. The white surface is rendered pebbly by intersecting striae, the longitudinal sculpture tending to twist spirally around the tube. A specimen in the Stanford University collection measures 250 mm. in total length, 15 mm. in diameter at the aperture. The geographic range seems to be between Guaymas and Acapulco, West Mexico. No living material was available for this study ; hence, the allocation of the species is highly tentative, especially as the shell has some points of resemblance both to *S. eruciformis* and to *Tripsycha tripsycha*.

Petaloconchus (Macrophragma) cereus Carpenter, 1857

P. cereus Carpenter, 1857*b* : 316, fig. 7. Philippines.

Holotype : B.M. (N.H.) Reg. No. 195920.

As Mörch commented, the type specimen is acid-etched and reveals a golden-yellow underlayer. The shell is regularly coiled and solitary, about 50 mm. in length. Some of the other British Museum specimens identified by Mörch show fine cancellate sculpture and appressed whorls.

Petaloconchus (Macrophragma) cochlidium Carpenter, 1857

P. cochlidium Carpenter, 1857*b* : 314, fig. 2. Australia.

Syntypes : B.M. (N.H.) Reg. No. 195921.

The syntype lot consists of a cluster of tightly coiled shells not unlike *P. flavescens* in appearance but dark brown in colour, with heavy lamellae, the upper double-keeled. Maximum diameter of the clump, 60 mm. ; length of one coiled individual, 20 mm. ; diameter of one tube, 1·2 mm.

Petaloconchus (Macrophragma) flavescens Carpenter, 1857

(Pl. 54, fig. 4)

P. flavescens Carpenter, 1857*b* : 314, fig. 3. "Sicily."

Syntype cluster : B.M. (N.H.) Reg. No. 195918.

As early as 1892 Monterosato pointed out that no such species is known in the Mediterranean, and it is not cited in the recent review of Sicilian vermetids by Priolo (1956*b*). However, anyone who has examined vermetids from the Guaymas-Mazatlán area of Mexico can recognize in this cluster a familiar form. The type lot having come from the Cuming collection makes its actual West American origin the more probable. Locally, the form is one of the commonest West Mexican vermetids. The *Turritella*-like tubes radiate outward in profusion, forming characteristically-shaped masses. The similar but much more loosely coiled *P.* (*M.*) *innumerabilis* Pilsbry & Olsson, 1935 (type locality, Tumbez, Perú) occurs also in the Guaymas-Mazatlán region, and only controlled laboratory studies will show whether the two are variants of a single species. The shells of *P. flavescens* vary in colour from terra-cotta to dark brown. Individual tubes are about 50 mm. in length, with a diameter at the aperture of 2 mm.

Petaloconchus (Macrophragma) lilacinus (Mörch, 1862)

Vermetus lilacinus Mörch, 1862*a* : 352. Zanzibar.

The type cluster of this form was from the Dunker collection, and may be in the Humboldt Museum, Berlin. Specimens of the " var. alpha " of Mörch, from Madagascar, are in the B.M. (N.H.) coll., Reg. No. 195922. They should probably best be considered hypotypes rather than syntypes. The shells are bright pinkish lavender, with weak laminae reduced to mere lirae in some tubes.

Petaloconchus (Macrophragma) macrophragma Carpenter, 1857

(Pl. 55, fig. 2)

P. macrophragma Carpenter, 1857*c* : 309. Mazatlán, Mexico.

Lectotype (here selected) : B.M. (N.H.) Reg. No. 57.6.4.1500.

The specimen is attached to a *Muricanthus*. It is small, tightly coiled, dark brown, strongly sculptured, and with an internal lamina.

In a recent discussion of Carpenter's material by Palmer (1958 : 172), a printer's error in assembling type has introduced ambiguity, which the reader of Palmer's paper can resolve by transferring the last six lines of the text under *P. macrophragma* to precede the last paragraph of the page. (Also, the generic heading "*Aletes*" and the following seven lines should precede the discussion of *A. squamigerus* on page 173.)

Petaloconchus (Macrophragma) nerinaeoides Carpenter, 1857

P. nerinaeoides Carpenter, 1857*b* : 316, fig. 6. Australia.

Syntypes : B.M. (N.H.) Reg. No. 195923.

The syntype lot is a cluster that shows a few laminae. Carpenter's illustration seems somewhat exaggerated as to their strength.

Petaloconchus (Macrophragma) octosectus Carpenter, 1857

P. octosectus Carpenter, 1857*b* : 317, fig. 8. South Africa ?

Holotype : B.M. (N.H.) Reg. No. 195924.

Length of the 5 volutions is about 30 mm. The coiling is not distinctive, and the locality remains open to doubt.

Petaloconchus (Macrophragma) renisectus Carpenter, 1857

P. renisectus Carpenter, 1857*b* : 315, fig. 5. Oceano Indica ?

Type material was not detected at the B.M. (N.H.) upon search in 1958. The variety *P. r. woodwardi* Carpenter (1857*b* : 316), from an unknown locality, is represented by a compact cluster showing some laminae (B.M. (N.H.) Reg. No. 19595). Mörch (1862*a* : 348) described it as "forma 1".

Petaloconchus (Macrophragma) varians (Orbigny, 1841)

Vermetus varians Orbigny, in 1834–46 : 456, pl. 54, figs. 7–10. Rio de Janeiro.

Syntype cluster : B.M. (N.H.) Reg. No. 54.12.4.533.

Orbigny's figures (reprinted by Tryon, 1886, pl. 47, figs. 22–23) are good. The syntype cluster measures about 56 mm. high by 55 mm. across. Two opercula are glued on a separate slide. They are thin and chitinous but too crushed to show whether they had the characteristic upstanding spiral lamellae. The tubes have *Macrophragma* coiling, though internal laminae are not evident. They resemble the Floridan *P. (M.) nigricans* (Dall) but are larger in diameter.

Dendropoma (Dendropoma) corrodens (Orbigny, 1842)

Vermetus corrodens Orbigny, 1841-42 : 235. Orbigny, 1845–53 ? : 129, pl. 18, figs. 1–3.

Syntypes : B.M. (N.H.) Reg. No. 54.10.4.159. Cuba.

Several specimens constitute the type colony, burrowing on the spire of an *Astraea tuber*. Most of the specimens are white ; a few are brown. The operculum, on a separate mount, shows the internal mamilla or button. Diameter of a typical coil, 6·5 mm.

Dendropoma (Dendropoma) dacostae (Mörch, 1860)

Spiroglyphus dacostae Mörch, 1860*a* : 46. East Indies.

Holotype : B.M. (N.H.) Reg. No. 195925. Figured by DaCosta (1771, pl. 11, fig. 15) ; figure reprinted by Tryon (1886, pl. 55, fig. 9).

The specimen is attached to what looks like a block of marble but is probably part of a large shell, perhaps a *Cassis*, that has been cut to leave only the immediate base of the vermetid. Although the apical whorls are missing, their spiral trench shows that this is a close relative of *D. maximum*. At the large end the tube is only lightly attached. It is brown within. Some spiral and longitudinal sculpture may be made out, and the junction of the shell with the substrate is scalloped.

Dendropoma (Dendropoma) leucozonias (Mörch, 1861)

Siphonium (*D.*) *leucozonias* Mörch, 1861 : 155. West Africa.

Lectotype (here selected) : B.M. (N.H.) Reg. No. 195926.

Solitary shells, with planorboid coiling, these are brown on the upper surface, white on the outer side of the whorl beyond the weak crest. Operculum red, conical, mamillate within. Diameter of a coil about 6·5 mm.

Dendropoma (Dendropoma) lituella (Mörch, 1861)

(Pl. 55, fig. 1)

Siphonium (*D.*) *lituella* Mörch, 1861 : 154. California.
? *S.* (*D.*) *megamastum* Mörch, 1861 : 153, pl. 25, figs. 12–13. California.

Lectotype (here selected) : B.M. (N.H.) Reg. No. 195917, on *Haliotis fulgens*.

The syntype colony of *D. lituella* consists of a number of separated individuals burrowing and well entrenched in the cortical layer of the *Haliotis*. The brown juvenile shell has 1½ volutions. On the largest adult there is a slight crest. This shell measures 6 mm. in maximum length of coil. The operculum is in a separate vial ; it is flat, with a frayed edge.

Mörch gave no indication as to the collection from which his type specimens of *S. megamastum* came, but they are evidently not among the British Museum holdings, for no specimens bearing Mörch's labels were found there upon search in 1958. The form was described as shallowly burrowing in a *Haliotis*. Mörch thought that he saw bristles on the outside of the operculum, as in *Stephopoma* (hence, the choice of the name *Dendropoma*, meaning " branched lid "). Long and diligent modern search having failed to bring such an operculum to light, it seems plausible to conclude that his supposed bristles were hydroid stalks or other agglutinated material on the scaly outer surface. Some specimens in the Stanford University collection have an operculum with tufts of sponge spicules that faintly resemble Mörch's sketches. Until his type specimens become available, it will be unwise to distinguish *D. megamastum* however much one would like to use the name for one of the two or more Californian vermetids that are clearly distinct from *D. lituella*.

Dendropoma (Dendropoma) platypus (Mörch, 1861)

Siphonium (*Stoa*) *platypus* Mörch, 1861 : 157.

Holotype : B.M. (N.H.) Reg. No. 195927. Hawaiian Islands, on a *Chama*.

The operculum, in place, is concave in form, as in *D. maximum*, which the shell resembles save that it is attached to another shell instead of being entrenched in coral. Mörch considered the operculum to be flatter than that of some others, but it now appears to be distinctly concave.

Dendropoma (Dendropoma) rastrum (Mörch, 1861)

(Pl. 54, fig. 2)

Vermiculus rastrum Mörch, 1861 : 180. No locality cited for shell.

Holotype : B.M. (N.H.) Reg. No. 195916.

The type material for this species is composite, consisting of a coarsely scaly, loosely coiling shell, without locality, and an operculum that Mörch assumed to have come from it. Other material that he had in hand, from Puntarenas, Costa Rica, probably influenced him in placing the species in *Vermiculus* (now *Vermicularia*). The operculum is not a vermetid operculum and probably is from a tropical West American *Vermicularia* (family Turritellidae). The shell itself, however, matches well a large form from California hitherto confused with "*Aletes*" *squamigerus* by Californian workers. It became evident that species representing two genera were masquerading under one name when, a few years ago, in the Stanford University collection, a *Dendropoma* operculum was observed in one tube of a cluster labelled "*A.*"*squamigerus*. Careful study of the entire contorted colony showed that the initial whorls were entrenched and *Dendropoma*-like in form and that the later whorls were a little corroded where one tube crossed another. Only a practised eye could distinguish the second species, so similar was the sculpture to that of *Serpulorbis squamigerus*. Mörch's holotype of "*V.*" *rastrum* corresponds perfectly with this otherwise nameless Californian form, and the recommendation is here made that it be regarded as probably Californian in origin, even though we lack the nuclear whorls and an authentic operculum to confirm unequivocally its position. None of the specimens available at Stanford University or in other collections studied have precise locality data, unfortunately, but the geographic range seems to be from central California southward to the northern part of Lower California. Specimens have been found attached in large clusters to soft rock as well as to such shells as *Haliotis*. Fully developed, the white tubes are heavy, as much as 10–12 mm. in diameter, and strongly sculptured with longitudinal rows of scales.

E. CHECK LIST OF WEST AMERICAN VERMETIDAE

It is to be hoped that with the aid of the clues given by this paper, other workers will undertake studies of the vermetids in areas of abundance. The present study was not begun with the intention of stressing any special geographic provinces, but as it progressed, one area became conspicuous for the occurrence of an unusual number of species and genera (with seven out of the presently-recognized ten generic units). A species list for this area—the west coast of North and Central America—seems appropriate, and it may serve as a start toward a more thorough review, which is now planned. The names of the species—most of which have already been mentioned—are arranged alphabetically, with original generic allocation, author, and date of proposal. Allocation in terms of the present classification is attempted (necessarily provisional for several forms) ; lastly, there are brief notes on the species not discussed elsewhere in this paper. [Generic names are abbreviated to initial letters, as follows : *D.*, *Dendropoma* ; *P.*, *Petaloconchus* ; *S.*, *Serpulorbis* ; *V.*, *Vermetus*.]

albida, *Bivonia*, Carpenter, 1857. Nuclear whorls only, probably indeterminate. Holotype in B.M. (N.H.).

angulatus, *Vermetus*, Chenu, 1844, *ex* Rousseau MS. ?*SERPULORBIS*. No type locality stated ; possibly not West American.

centiquadrus, *Vermetus*, Valenciennes, 1846. *VERMETUS*, *s.l.*, probably West Mexico.

compacta, *Bivonia*, Carpenter, 1864. *V.* (*THYLAEODUS*) (?). Type locality, Vancouver Island area.

complicatus, *Petaloconchus*, Dall, 1908. *P.* (*MACROPHRAGMA*).

contorta, *Bivonia*, Carpenter, 1857. *V.* (*THYLAEODUS*).

effusus, *Vermetus*, Chenu, 1844, *ex* Valenciennes MS. ?*SERPULORBIS*. No type locality stated ; possibly not West American.

eruciformis, *Thylacodes*, Mörch, 1862. *S.* (*SERPULORBIS*).

flavescens, *Petaloconchus*, Carpenter, 1857. *P.* (*MACROPHRAGMA*).

imbricatus, *Aletes*? *centiquadrus*, Carpenter, 1857. Type specimen, B.M. (N.H.), probably indeterminate ; juvenile.

indentata, *Bivonia*? *contorta*, Carpenter, 1857. *V.* (*THYLAEODUS*).

innumerabilis, *Petaloconchus*, Pilsbry & Olsson, 1935. *P.* (*MACROPHRAGMA*).

lituella, *Siphonium*, Mörch, 1861. *D.* (*DENDROPOMA*).

macrophragma, *Petaloconchus*, Carpenter, 1857. *P.* (*MACROPHRAGMA*).

margaritaceus, *Vermetus*, Chenu, 1844, *ex* Rousseau MS. *S.* (*CLADOPODA*).

margaritarum, *Vermetus*, Valenciennes, 1846. = *S. MARGARITACEUS*.

megamastum, *Siphonium*, Mörch, 1861. = *D. LITUELLA*.

montereyensis, *Petaloconchus*, Dall, 1919. *P.* (*MACROPHRAGMA*). California, from Monterey southward.

oryzata, *Thylacodes*?. Mörch, 1862. *S.* (*CLADOPODA*) (?).

panamensis, *Vermetus*, Chenu, 1844, *ex* Rousseau MS. *S.* (*SERPULORBIS*).

peronii, *Vermetus*, Chenu, 1844, *ex* Rousseau MS. *S.* (*SERPULORBIS*). No type locality stated ; possibly not West American. Not *V. peronii* of Valenciennes, 1846, which is probably *V. centiquadrus*.

rastrum, Vermiculus, Mörch, 1861. *D.* (*DENDROPOMA*).

squamigerus, Aletes, Carpenter, 1857. *S.* (*SERPULORBIS*). California and southward to southern Baja California.

sutilis, Bivonia, Mörch, 1862. ?*SERPULORBIS*. Holotype in B.M. (N.H.).

tripsycha, Vermetus, Pilsbry & Lowe, 1932. *TRIPSYCHA*.

tulipa, Vermetus, Chenu, 1843, *ex* Rousseau MS. *S.* (*SERPULORBIS*) (?). No type locality stated ; possibly not West American.

F. EVOLUTION OF THE VERMETIDAE

The earliest fossil that may possibly qualify as a vermetid is of Upper Cretaceous age. However, the preservation is not good enough to permit its unqualified acceptance as a gastropod. Some of the Lower Eocene fossils, from the Cuisian of France, are unquestionably vermetid, for they show clearly the scars of broken feeding tubes characteristic of several vermetid groups. The coiling of these shells suggests that of the genus *Serpulorbis*. Several similar species occurred in Europe during Middle and Upper Eocene time, and there were a few—perhaps only two—on the Gulf Coast of the United States. The genus continued to be represented throughout the Tertiary in Europe. By early Miocene time, *Petaloconchus*, with its internal spiral lamellae, had appeared in Europe as well as in the Caribbean area. *Dendropoma* is not so easily recognized in the fossil state, but *Elliptovermetus*, which seems to be an extinct subgenus of it, appeared in the Upper Oligocene of France.

We cannot trace directly the evolutionary history of nuclear whorls and opercula, as these are difficult or impossible to obtain fossilized, but some hint as to their pattern of development may be gained by a study of the range of form of these structures in modern vermetids, as shown in the various figures given here. The nuclear whorls of some *Macrophragma* species and some *Serpulorbis* are almost indistinguishable. This may represent the primitive form, away from which most of the groups have moved in different directions and to diffierent degrees, *Dendropoma* seeming to have diverged farthest. The same is true also for opercula. Hence, we may conclude that the evidence of the fossil record is at least not inharmonious with that derived from the study of living forms.

G. ACKNOWLEDGMENTS

During the more than twelve years since Professor T. A. Stephenson's first request for an identification set me to studying the Vermetidae, I have had much fruitful exchange of letters and ideas with Professor John E. Morton, whose paper will flesh out the bare bones of the present taxonomic treatment.

I wish to express to the officials of the British Museum (Natural History) my gratitude for the privilege of studying type material under their care and for permission to publish the photographs of several hitherto unfigured forms. These excellent pictures were made in the Photographic Section of the Museum. Mr. Peter Dance and Mr. Ian Galbraith, of the Mollusca Section, were especially helpful in making my stay worthwhile, and I appreciated their many thoughtful courtesies.

My debt to M. Igor Marche-Marchad has been mentioned above, for having provided topotypes—taken alive—of (among others) the type species of *Vermetus*, from West Africa. I am indebted also to Mr. James H. McLean, student at Stanford University, for some topotypes from West Mexico. Grateful acknowledgment, too, should go to the many colleagues who have sent vermetid specimens for my study, such background material having been invaluable in a review of the whole family.

Line drawings used as Text-figures in this paper were prepared by Mr. Perfecto Mary, technician in the Department of Geology, Stanford University.

Two funds at Stanford University defrayed the costs of my trip to London in 1958, one supplied by an anonymous donor, the other from the Shell Oil Company's Grant for Scientific Research. Thus, I was privileged to handle the actual material studied a century ago by Carpenter and by Mörch, two authors of important systematic works on Vermetidae. More recently, an advantage came to me that neither of them had—first-hand study of these molluscs in an area where they are abundant. Through the kind auspices of the Belvedere Scientific Fund of San Francisco, California, I had a few days of observation and collecting at La Paz, Baja California, which afforded fresh insights into vermetid relationships and made a fitting climax to my several previous years of museum study.

For all this aid, so generously given, my thanks. One may hope that as a result, the Vermetidae will regain the esteem of malacologists and will not again be accorded a century of disregard.

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PLATE 54

FIG. 1. *Serpulorbis oryzata* (Mörch). Holotype. British Museum (Nat. Hist.) Reg. No. 195912. ×0·7. Diameter of aperture, 15 mm.

FIG. 2. *Dendropoma rastrum* (Mörch). Holotype. B.M. (N.H.) Reg. No. 195916. ×1·3. Diameter of aperture, 9 mm.

FIG. 3. *Serpulorbis eruciformis* (Mörch). Holotype. B.M. (N.H.) Reg. No. 195915. ×1·3. Diameter of aperture, 7 mm.

FIG. 4. *Petaloconchus* (*Macrophragma*) *flavescens* Carpenter. Syntypes. B.M. (N.H.) Reg. No. 195918. ×2·6. Diameter of aperture, 1·5 mm.

PLATE 55

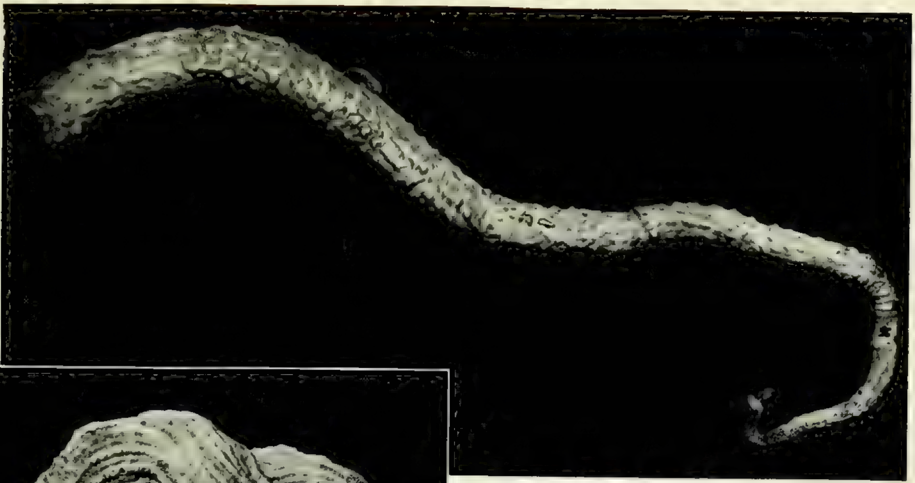
FIG. 1. *Dendropoma lituella* (Mörch). Lectotype (upper specimen), on *Haliotis*, the photograph retouched to block out a number of extraneous tubicolous annelids of the genus *Spirorbis*. B.M. (N.H.) Reg. No. 195917. ×4. Diameter of aperture, 1·5 mm.

FIG. 2. *Petaloconchus* (*Macrophragma*) *macrophragma* Carpenter. Lectotype (central specimen). B.M. (N.H.) Reg. No. 57.6.4.1500. ×3. Diameter of aperture, 1 mm.

FIG. 3. *Vermetus* (*Thylaeodus*) *contortus* (Carpenter). Lectotype. B.M. (N.H.) Reg. No. 57.6.4.1490. ×3. Diameter of aperture, approximately 3 mm.

FIG. 4. *Vermetus* (*Thylacodus*) *indentatus* (Carpenter). Lectotype. B.M. (N.H.) Reg. No. 57.6.4.1494. ×3. Diameter of aperture, 1·5 mm.

FIG. 5. *Serpulorbis squamigerus* (Carpenter). Syntypes. B.M. (N.H.) Reg. No. 55.3.14.57. ×1. Diameter of aperture, 9 mm.



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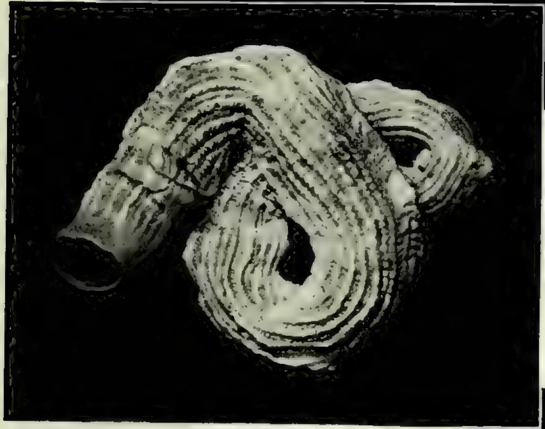

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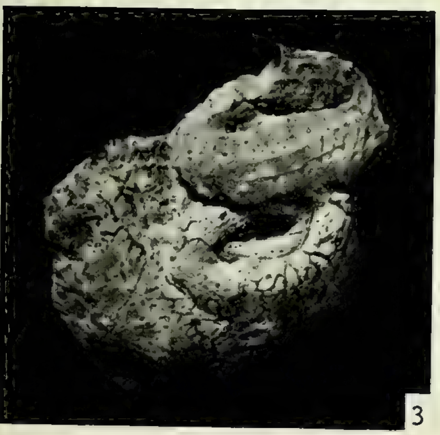

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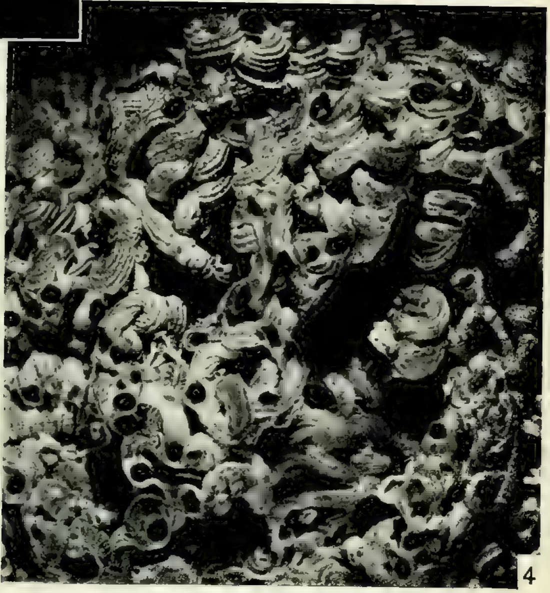

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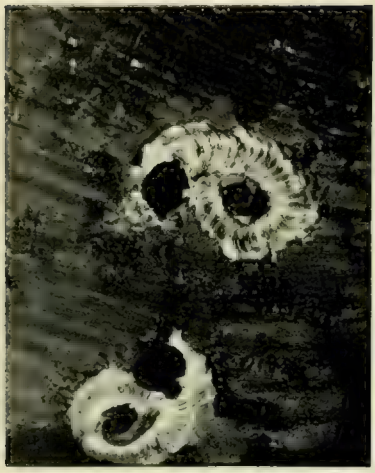

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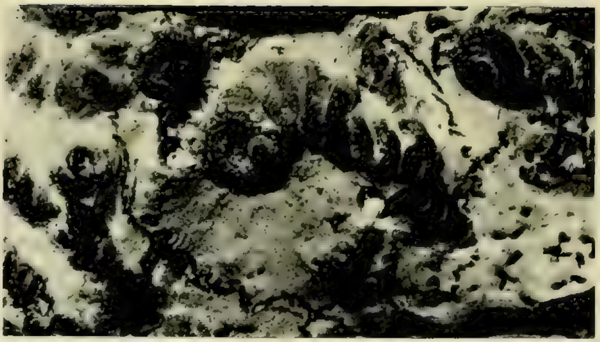

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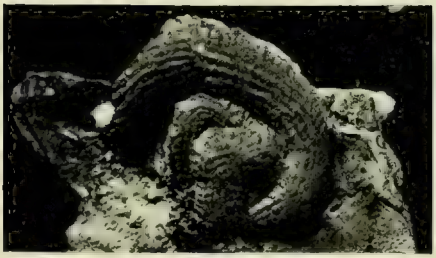

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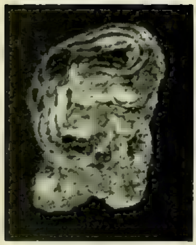

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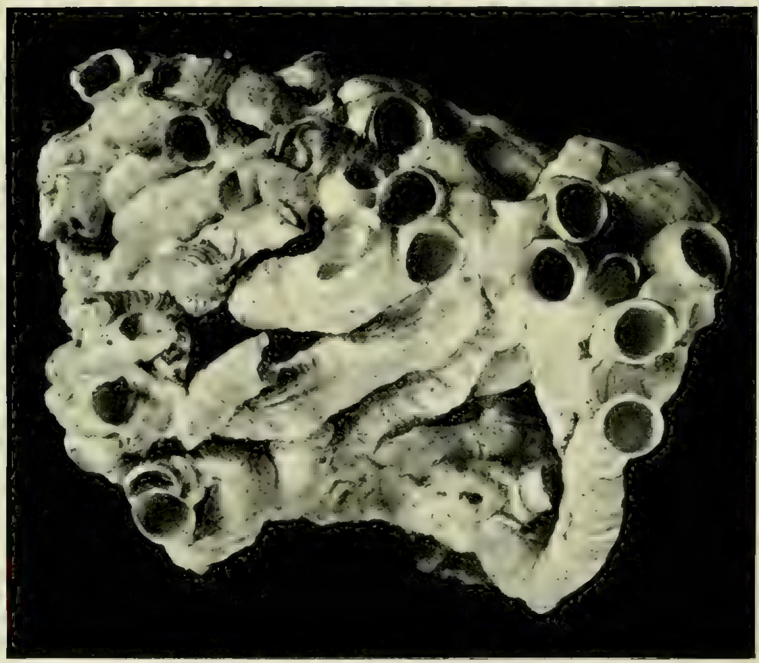

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A REVISION OF THE GENUS *DINOTOPTERUS* BLGR. (PISCES, CLARIIDAE) WITH NOTES ON THE COMPARATIVE ANATOMY OF THE SUPRABRANCHIAL ORGANS IN THE CLARIIDAE

10 FEB 1961
PRESENTED

P. H. GREENWOOD

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LONDON : 1961

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1961

BY

P. H. GREENWOOD

Department of Zoology, British Museum (Natural History)

Pp. 215–241 ; 1 *Text-figure*

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By P. H. GREENWOOD

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INTRODUCTION

The genus *Bathyclarias* was created by Jackson (1959) to accommodate ten endemic species of predominantly deep-water Clariidae from Lake Nyasa. Anatomical work which I have carried out on Jackson's material, and on other specimens, leads me to conclude that *Bathyclarias* does not differ substantially from the genus *Dinotopterus* (Boulenger, 1906). At present, *Dinotopterus* is a monotypic genus confined to Lake Tanganyika; a second species, *D. jallae* G. & T., 1917 from Southern Rhodesia should be referred to the genus *Clarias* (R. A. Jubb, personal communication).

THE GENERA *DINOTOPTERUS* AND *BATHYCLARIAS*

No comprehensive definition of *Dinotopterus* has been published. Combining published descriptions and observations on specimens of *D. cunningtoni*, the genus can be distinguished from other clariids by the following characters: sides of head incompletely enclosed by bone, there being an appreciable gap between the supraorbital, dermosphenotic and sphenotic bones; eyes laterally placed, forming part of the head outline when the fish is viewed from above; no arborescent organs present in the suprabranchial chamber (this character was first observed by Poll [1953]; other accounts of the genus [David, 1935; Marlier 1938; Bertin & Arambourg, 1958] imply that the arborescent organs are well developed); a small adipose dorsal fin present.

The last character calls for some comment. In all but the smaller specimens of *D. cunningtoni*, the fin is poorly developed; it is little more than a slightly thickened and humped upper margin to the caudal peduncle. However, contrary to Boulenger's opinion, the fin is supported by the elongated neural spines of the posterior caudal vertebrae. These spines are *c.* 1·3–1·5 times longer than those of the preceding vertebrae. Thus, although superficially the adipose dorsal fin of adult *D. cunningtoni* is not a striking character, its presence is clearly manifest in the underlying bony structure.

The most outstanding morphological characters of *Bathyclarias* are the laterally placed eyes and the greatly reduced or even non-existent arborescent organs; that is to say, characters which distinguish *Bathyclarias* from *Clarias* but not from *Dinotopterus*. Only two characters given by Jackson (op. cit.) seem to separate *Bathyclarias* and *Dinotopterus*, namely " sides of head enclosed in bony shields " and ". . . no adipose fin present." The former is not correct; the arrangement of the lateral roofing bones in all species of *Bathyclarias* conforms to the *Dinotopterus* pattern, with a large space separating the supraorbital, dermosphenotic and sphenotic bones. The thickened cephalic skin gives a superficial appearance of continuity but when the skin is removed, the true relationship of the bones is revealed.

The question of presence or absence of an adipose dorsal fin is more equivocal. Species referred to *Bathyclarias* show considerable variation in the posterior extension of the dorsal fin; in some, it is narrowly separated from the caudal whilst in others there is a longer gap. In none is the distance separating the two fins as great as it is in *Dinotopterus cunningtoni*. I have examined all the available material of *Bathyclarias* and conclude that in some (those with the greatest dorsal-caudal interspace) a weakly developed adipose fin is visible externally. In these fishes the upper caudal peduncle margin is thickened and, in a few, its outline is slightly humped. In none is the adipose fin as obvious as in *Dinotopterus cunningtoni* of the same size. However, the osteological picture is more convincing. I have examined radiographs of two *Bathyclarias* representing species with long and short dorsal-caudal interspaces. In both species the most posterior caudal vertebrae have elongate neural spines which are clearly longer than those of the preceding vertebrae underlying the rayed dorsal. Comparison between the more posterior caudal vertebrae of *Dinotopterus cunningtoni* and the two *Bathyclarias* species shows that the latter have relatively shorter neural spines (*c.* 1·3 × longer than the preceding spines; cf. 1·3–1·5 × in *D. cunningtoni*). Despite these differences, I consider that the state of caudal peduncle development represented in the two *Bathyclarias* species serves to bridge the gap between the presence and absence of an adipose fin.

An identical situation exists within the genus *Clarias* (see David op. cit.). Here, three species of the subgenus *Heterobranchoides*, *Clarias mellandi* Blgr., *C. ngamensis* Casteln., and *C. pentissgrayi* (Fowler), all exhibit traces of an adipose fin. Again, the fin is poorly differentiated externally but is supported by elongate neural spines. The osteology of the skull in these fishes is typically that of a heterobranchoid *Clarias*, as is the condition of the hypertrophied suprabranchial arborescent organ (*C. ngamensis* and *C. mellandi* from personal observations, *C. pentissgrayi* from Fowler's [1931] description which does not include the suprabranchial organs). Certainly the " adipose " fin in *C. mellandi* and *C. ngamensis* is comparable, externally, with the dorsal thickening of the peduncle found in many *Bathyclarias* species. Furthermore, the condition of the supporting neural spines in *C. mellandi* (the only species examined for this character) is comparable with that found in the *Bathyclarias* species mentioned above.

Thus it seems that the presence or absence of a small adipose dorsal fin can no longer be considered sufficiently trenchant to warrant its use as the sole criterion for separating *Dinotopterus* and *Bathyclarias*.

One other point may be touched upon here. That is, the condition of the suprabranchial organ in the two " genera ". In *Dinotopterus cunningtoni* the arborescent organs, so characteristic of the genus *Clarias*, are not developed, even in the largest specimens. In *Bathyclarias* the various species provide examples of development covering the entire range, from complete absence through simple stumps and sparsely branched " trees " to arborescent organs closely approaching the *Clarias* type in size and complexity. This wide range of variation in suprabranchial structure is described and discussed on p. 231–240.

If all these characters are considered, there seem to be no anatomical grounds for recognizing two genera and I propose to treat *Bathyclarias* Jackson, 1959 as a synonym of *Dinotopterus* Blgr., 1906, a redescription of which is given below.

THE GENUS *DINOTOPTERUS* BOULENGER, 1906

Dinotopterus Blgr. 1906, *Trans. zool. Soc. Lond.* **17** : 550; *Idem. Cat. Afr. Fish.*, 1911, **2** : 276; David, 1935, *Rev. Zool. Bot. Afr.* **28**, 95 (misspelt *Dinopterus*). *Clarias*, part (*C. nyasensis* and *C. longibarbis*) Worthington, 1933, *Proc. zool. Soc. Lond.*, 285. *Bathyclarias* Jackson, 1959, *Proc. zool. Soc. Lond.* **132** : 109–138.

TYPE SPECIES. *Dinotopterus cunningtoni* Blgr., 1906.

Clariid fishes with the lateral roofing bones of the skull not forming a continuous casque because the supraorbital, sphenotic and dermosphenotic are separated by a distinct space. Eyes lateral, forming part of the head outline when viewed from above. Dorsal and caudal fins separated by a distinct space which, at least superficially, shows all stages of intergradation between a weakly-developed adipose fin and the complete absence of such a fin ; whether the fin is clearly developed or not, the more posterior caudal vertebrae have relatively elongated neural spines.

Suprabranchial chamber always present, as are the " gill-fans " forming its lateral and ventral walls ; suprabranchial arborescent organs variously developed, from completely absent to moderately large and much branched.

DISTRIBUTION. Lakes Tanganyika and Nyasa : essentially a lacustrine genus, rarely occurring in streams and rivers.

THE LAKE TANGANYIKA SPECIES, *DINOTOPTERUS CUNNINGTONI* BLGR., 1906

This species was recently redescribed by Poll (1953) ; in this description he remarks that the suprabranchial cavity is without arborescent organs. In general, this statement is correct but requires some amplification. None of the specimens I have examined possesses large or many-branched trees of the *Clarias* type, but a small stump or knob may be present on the fourth gill-arch of both large and small fishes. In some small specimens this structure is relatively large and bifid, occupying a fair volume of the cavity ; in others, it is reduced to a slight swelling. No external indication of a knob is apparent in fishes with a head length of less than 0·7 cm. (at which size the " gill-fans " are still incompletely developed). In four specimens with head lengths of 1·4–3·5 cm. a well-developed knob is present on the epibranchial of the fourth arch. The next largest specimen available (standard length 17·5 cm.; head 4·7 cm.) has completely developed " gill-fans " but no trace of an arborescent organ.

Of particular interest is an apparently ontogenetic change in the histology of the suprabranchial epithelium (see p. 235 for a full explanation of the terms used). In young *D. cunningtoni* (smallest fish examined, 11·8 cm. S.L.) the gill tissue in this epithelium is arranged in the " Clarias " pattern of regular but sinuous lines or lamellae. Such is also the condition in fishes up to 17·5 cm. S.L. But, in the next larger specimen (46·5 cm. S.L.) and in all larger fishes, the lamellae are arranged in the " coralline " pattern of small circular patches of gill-cells. Unfortunately, I have not found any specimen in an intermediate condition, although in two of the smaller fishes (12·5 and 17·5 cm. S.L.), a few lamellae are in the form of elongate ovals. These could be interpreted as having arisen from the union of two neighbouring lamellae in a " Clarias "-type pattern. Subsequent development may involve the fractioning, by union at several points, of these ovals.

The only other *Dinotopterus* species (*D. worthingtoni*) for which a wide size range is available, does not show any difference in lamellar pattern between large and small fishes. Because the adult size of *D. worthingtoni* is considerably less than that attained by *D. cunningtoni*, ontogenetic changes might take place at a size smaller than any represented in the collection.

THE SPECIES OF *DINOTOPTERUS* OCCURRING IN LAKE NYASA

Jackson (1955 and 1959) gave the first detailed account of the remarkable species-flock of Clariidae in Lake Nyasa. In his later paper, he drew attention to several taxonomic points which still required further study. On the basis of Jackson's original material, supplemented by other specimens collected by J. F. R. O., the Survey party of 1939 and Dr. Rosemary Lowe-McConnell, I have been able to investigate these points and also expand the descriptions of certain species.

My primary interest in the Nyasa *Dinotopterus* lay in their peculiar suprabranchial organs (see p. 232) ; when more material became available it was clear that the condition of these structures was more variable, both inter- and intraspecifically, than I had led Mr. Jackson to believe (see Jackson, 1959, p. 112). Furthermore, the suprabranchial organ showed itself to be a character of some taxonomic importance. A brief description of the suprabranchial region is now given for each species and should be read in conjunction with Tables I and II, and with the detailed account on pp. 231–240. Certain new descriptive terms are defined in that section.

Dinotopterus nyasensis (Worthington), 1933

Clarias nyasensis Worthington, 1933, *Proc. zool. Soc. Lond.*, 308, fig. 9.
Bathyclarias nyasensis (part), Jackson, 1959, *Proc. zool. Soc. Lond.* **132** : 113.

Lectotype. B.M. (N.H.) Reg. No. 1932.11.15. 584.

The so-called " smooth-headed " form of this species (Jackson, 1959) is now recognized as a distinct species (see p. 222). Within *D. nyasensis* as defined here there is considerable variation in the roughness of the skull. Three small specimens, (27, 33 and 39 cm. S.L.) have the roofing bones almost completely smooth except for a few scattered tubercles on the occipital and frontal regions of the skull. In larger fishes the skull is entirely rugose, but in the largest specimen examined the rugosity is like that of the three smallest fishes. Such cyclical ontogenetic changes in skull ornamentation seem common amongst the larger Clariidae (personal observations).

As the additional material does not otherwise differ from the descriptions given by Worthington (1933) and Jackson (1953) a full redescription of the species is not warranted.

SUPRABRANCHIAL ORGAN. The suprabranchial cavity is large ; its length is about 33% of the head in fishes 49–62 cm. standard length (see also Table II). The arborescent organs, on the other hand, are poorly developed. In a fish of head length 20 cm. the tree on gill-arch II is polyfid and about 12 mm. high, that on arch IV about 16 mm. high and more extensively branched. In a smaller individual (H.L. 8·3 cm.) no tree is developed on the second arch and that of the fourth arch is a low, bifid stump. Such variability is not entirely size-correlated ; for example, a specimen of 21 cm. head length has trees substantially less developed than another individual of 18 cm. H.L. In this fish, the trees are almost as well developed as in a specimen of 23 cm. head length.

The epithelium lining the suprabranchial cavity is highly vascular and the gill-like tissue is distributed in the " Saccobranchus " pattern (see p. 235).

Dinotopterus jacksoni sp. nov.

Bathyclarias nyasensis (part), Jackson, 1959, *Proc. Zool. Soc. Lond.* **132** : 113 (the smooth-headed forms only).

Bathyclarias loweae (part). *Idem, ibid.*, 114, fig. 1B.

HOLOTYPE. A fish 61 cm. standard length, from Nkata Bay ; B.M. (N.H.) Reg No. 1960.2.29.26.

DESCRIPTION. Based on the holotype, two entire specimens 46 and 68 cm. S.L., and one head 23·3 cm. long.

Length of head contained 3·1–3·8 times in standard length, the dorsal surface smooth or relatively smooth ; when present, the rugose areas are most apparent on the posterior and antero-lateral regions of the skull. In large specimens the squamosal region (i.e. the sphenotic and pterotic bones) is slightly domed ; the intervening occipital region is flat. Frontal and occipital fontanelles barely visible beneath the thick cephalic skin ; the frontal fontanelle very narrow, the occipital fontanelle almost circular. Head broad, its width contained 4·4–4·9 times in standard length and 1·4–1·6 times in head length. Eye lateral, its diameter 15·8–18·8 in head length and 9·8–10·5 in the interorbital width, which is contained 1·6–1·9 times in head length and is about equal to the width of the mouth. Dorsal outline of the snout rounded ; snout length contained 3·7–4·4 in the head.

Barbels smooth, the base of the maxillary pair somewhat fleshy. Length of nasal barbel 1·9–4·5 in head ; maxillary barbel 1·3–1·7, outer mandibular 1·3–2·8, inner mandibular 2·2–5·3 in head. Barbel length shows negative allometry with head length.

Premaxillary and vomerine teeth fine and pointed ; length of half the premaxillary band 4·7–5·2 in head length, that of half the vomerine band 5·0–5·9 ; vomerine band interrupted in the mid-line, its width equal to or slightly less than that of the premaxillary band.

Gill rakers long (almost equal to the longest gill filaments) and numerous, 172–230 on the first gill-arch, the number showing positive correlation with standard length. In preserved material the gill filaments are colourless.

Dorsal fin with 64 rays, the distance between its origin and the supraoccipital contained 3·8–4·6 times in head length. Anal with 44 rays. Both fins are clearly distinct from the caudal. Pectoral fins short and covered with thick skin, the anterior face of the spine weakly denticulate or smooth ; greatest length of the pectoral contained 2·2–2·8 in head length. Caudal peduncle as long as deep to 1·4 times deeper than long. Adipose dorsal weakly developed.

Vertebrae (excluding the fused anterior mass) in the single specimen radiographed (the Type), 54.

I have great pleasure in naming this species after Mr. P. B. N. Jackson, who first recognized that certain specimens he referred to *Bathyclarias nyasensis* might represent a new species.

SUPRABRANCHIAL ORGANS. The suprabranchial chamber is moderately large (its length *c.* 32% of head ; see Table II for volumes) and the gill-fans are well developed. The arborescent organs are greatly reduced. In the three largest specimens there is no macroscopic indication of an anterior tree and the posterior one is represented by a simple, short phallic outgrowth. There is no posterior tree in the smallest specimen (S.L. 46 cm.) but there is a small stump occupying the usual site of the anterior tree.

Gill tissue in the suprabranchial epithelium is arranged in the " Saccobranchus " pattern. A striking feature in the histology of this epithelium is an abundance of large mucous cells widely distributed amongst the gill tissue and the undifferentiated epithelial cells.

Discussion. From Jackson's arrangement of the Nyasa species now referred to *Dinotopterus*, *D. jacksoni* is closely related to *D. nyasensis* and *D. loweae*. Indeed, specimens of *D. jacksoni* were previously included in both these species, although Jackson did stress the possibility that smooth-headed specimens of *Bathyclarias nyasensis* might represent a distinct species. At first sight the virtually smooth head of *D. jacksoni* seems a distinctive character, but as Jackson noted, this condition intergrades with that occurring in large *D. nyasensis*. Also, the skull of the smallest *D. jacksoni* specimen is as rough as that of a comparably sized *D. nyasensis*. From the examination of numerous *Clarias mossambicus* skulls and the skulls of most *Dinotopterus* species, it seems that the degree of rugosity is chiefly dependent on the size of the individual. The smooth-headed *D. gigas* may prove exceptional to this generalization (see also p. 221).

The principal difference between *D. nyasensis* and *D. jacksoni* lies in the greatly reduced suprabranchial structure of the latter. Although the arborescent organs of *D. nyasensis* are reduced, in no adult specimen is the reduction so marked as in *D. jacksoni*.

Two other, less pronounced, differences are the shorter pectoral fins of *D. jacksoni* and the tendency in this species for the squamosal region of the skull to become domed.

Even though *D. jacksoni*, *D. loweae* and *D. nyasensis* are closely related on " key " characters, I do not think that this reflects the phyletic relationship of the species ; more material is required, however, before this problem can be investigated.

Dinotopterus loweae (Jackson), 1959

Bathyclarias loweae (part) Jackson, 1959, *Proc. zool. Soc. Lond.* **132** : 114, fig. 1A.

One of the two specimens from which the original description was made is now referred to *D. jacksoni*. The redescription is based on the holotype (82 cm. S.L.), two other fishes 71 and 72 cm. S.L. and two heads 17·0 and 17·6 cm. long. A juvenile specimen 19·5 cm. S.L. is tentatively determined as *D. loweae*, but is not included in the description.

Holotype. B.M. (N.H.) Reg. No. 1960.2.29.3 from Nkata Bay.

Description. Length of head contained 3·1–3·7 times in standard length, its dorsal surface moderately rugose on the posterior half, smooth anteriorly. Head width contained 4·9–5·3 times in standard length and 1·4–1·7 times in head length. Eye diameter 14·2–18·0 in head length and 6·9–10·3 in interorbital width (showing negative allometry with head length). Interorbital width 1·8–2·1 in head length, snout length 3·5–4·4; distance between anterior nostrils 3·5–4·2 times. Barbels smooth; length of nasal barbel 3·0–4·3 in head, maxillary barbel 1·3–1·7, outer mandibulars 1·9–2·2, inner mandibulars 2·7–3·7 in head.

Premaxillary and vomerine teeth fine and pointed, length of half premaxillary band contained 4·5–5·7 times in head length, that of half vomerine band 4·5–6·5 times; vomerine band interrupted in the mid-line, its width equal to or slightly greater than that of the premaxillary band.

Gill rakers numerous and fine, from 180 (in fishes of 15·6 cm. H.L.) to 260 (H.L. 23·2 cm.); length 0·7–1·0 of the length of the longest gill filament (see also Jackson, 1959, p. 113).

Dorsal fin with *c.* 63–65 rays, the distance from its origin to the occiput contained 3·7–4·9 times in head length. Anal fin with 49–54 rays. Caudal peduncle 1·1–1·5 times as deep as long.

The strongly humped body of the holotype is less marked in other specimens and may thus be correlated with size or may be due to *post-mortem* muscular contraction.

SUPRABRANCHIAL ORGAN. The suprabranchial cavity is large (see Table II) and the arborescent organs well developed and much branched in all the specimens examined. In the smallest fish (a specimen 19·5 cm. S.L. and only tentatively placed in this species) the future anterior tree appears as a low swelling on the second gill-arch whilst the posterior tree is four-branched and is 3 mm. high.

Gill tissue in the suprabranchial epithelium is arranged in the " Clarias " pattern (see p. 235).

Dinotopterus ilesi (Jackson), 1959

Bathyclarias ilesi Jackson, 1959, *Proc. zool. Soc. Lond.* **132**: 116, fig. 2.

HOLOTYPE. A male 66 cm. S.L. from Nkata Bay, B.M. (N.H.) Reg. No. 1960. 2.29.8.

This description is based on the holo- and paratypes (66 and 59 cm. S.L. respectively) and one other specimen, 69 cm. S.L.

Length of head 3·2–3·3 in standard length, the dorsal surface rugose in the smaller specimens, smoother in the largest fish. Head width 4·7–5·1 in standard length and 1·4–1·6 in head length. Eye diameter 16·0–19·6 in head length and 10·0–10·5 in interorbital width, which is contained 1·7–1·9 times in the head. Snout length 3·9–4·1; distance between anterior nostrils 3·7–3·9 in head.

Barbels smooth, base of the maxillary barbel somewhat swollen. Length of nasal barbel 4·1–5·7, maxillary barbel 1·8–2·1, outer mandibular 3·7–4·8, inner mandibular 2·4–3·1 in head length.

Premaxillary and vomerine teeth fine and pointed, length of half premaxillary band about 5 in head. Vomerine band interrupted in the mid-line and slightly narrower than the premaxillary band, its half length contained 4·5–5·0 times in the head.

Gill rakers *c.* 0·8 length of longest gill filament; 170–184 on the first arch. Filaments dark, purplish-black (cf. *D. atribranchus*, *D. filicibarbis* and *D. worthingtoni*).

Dorsal fin with 65–67 rays, rather narrowly separated from the caudal; distance between its origin and the occipital process contained 3·8–4·5 times in the head length. Anal fin with 50–52 rays. Caudal peduncle 1·1–1·6 times as deep as long.

The " black removable mucus over the body " which Jackson notes, is not easily discernible in preserved material.

SUPRABRANCHIAL ORGAN. The suprabranchial cavity is large (see Table II), the arborescent organs present and much branched. There is considerable individual variation in the size of the trees; those of the type (66 cm. S.L.) are much smaller than the trees in the paratype (59 cm. S.L.).

Gill tissue in the lining epithelium is arranged in the " Saccobranchus " pattern (see p. 235).

Dinotopterus longibarbis (Worthington), 1933

Clarias longibarbis Worthington, 1933, *Proc. zool. Soc. Lond.* 309; fig. 10.
Bathyclarias longibarbis, Jackson, 1959, *Proc. zool. Soc. Lond.* **132** : 117.

HOLOTYPE. A male 75 cm. S.L. B.M. (N.H.) Reg. No. 1932.11.15. 592.

DESCRIPTION. Based on the holotype and two other specimens, 44·5 and 40·5 cm. S.L.

Length of head 3·4–3·7 in standard length, dorsal surface rugose, especially over the posterior two-thirds. Width of head contained 1·4–1·5 in head length. Eye diameter 14·0–14·7 in head length, 7·4–8·8 in interorbital width which is contained 1·6–1·9 in head. Snout 3·5–3·6 in head length; distance between anterior nostrils 3·6 times.

Barbels long and smooth, length of nasal barbel contained 1·1–1·6 times in head, maxillary and outer mandibular barbels respectively 1·2–1·3 and 1·1–1·2 times as long as the head; inner mandibular barbels 1·2–1·6 in head. It is interesting to note that the negative allometry of barbel length with standard length usual in other species is not at all marked, despite the size discrepancy between the type and the two smaller specimens.

Premaxillary and vomerine teeth fine and pointed, half length of either band contained about 5 times in head length. Vomerine band narrowed medially but continuous in two specimens, interrupted in the third, its width slightly less than that of the premaxillary band.

Gill rakers relatively short, about 0·5–0·6 of the length of the longest gill filaments; there are, on the first gill arch, 145 rakers in the type (75 cm. S.L.); 90 and 83 rakers in the two smaller fishes (S.L's. 44·5 and 40·5 cm. respectively).

Dorsal fin with *c.* 65 rays, distance from its origin to the occiput contained 5 times in the head. Anal fin with *c.* 56 rays. Caudal peduncle 1·4 times as deep as long.

SUPRABRANCHIAL ORGAN (see also Table II). A good ontogenetic series is provided by this material. The type specimen has large, polyfid arborescent organs on both the second and fourth arches. In the fish 44·5 cm. S.L., the anterior tree is merely a stub, whilst the posterior tree is small, with seven branches. A similar developmental state is seen in the 40·5 cm. fish, except that the anterior tree is even less developed.

Gill tissue in the suprabranchial epithelium is distributed in the " Clarias " pattern.

Dinotopterus rotundifrons (Jackson), 1959

Bathyclarias rotundifrons Jackson, 1959, *Proc. zool. Soc. Lond.* **132** : 118. fig. 3.

HOLOTYPE. B.M. (N.H.) Reg. No. 1960.2.29.11, from Nkata Bay.

As there are no additional specimens, reference is made to the original description.

SUPRABRANCHIAL ORGAN. The cavity is relatively small (see Table II) and the arborescent organs are greatly reduced. There is no macroscopic indication of an anterior tree and the posterior tree is represented by a single, phallic projection about 5 mm. high (i.e. in a specimen of 14·5 cm. head length).

Gill tissue in the suprabranchial epithelium is arranged in a " coralline " pattern (see p. 236).

Dinotopterus foveolatus (Jackson), 1955

Clarias foveolatus Jackson, 1955, *Proc. zool. Soc. Lond.* **125** : 681, text-fig.
Bathyclarias foveolatus, *Idem*, 1959, *Ibid.* **132** : 118.

The only information additional to that given by Jackson (op. cit.) concerns the structure of the suprabranchial organs.

Jackson was misled by the well-developed " gill fans " into stating " Accessory breathing organs present, as is usual in this family . . .".

The suprabranchial chamber of *D. foveolatus* is considerably reduced, its length being only about 20% of the head. There is a corresponding decrease in depth so that the chamber is noticeably shallow (see Table II). No appreciable reduction is apparent in the " gill-fans ". The tree associated with the fourth gill arch is reduced to a small " T "-shaped outgrowth and there is no macroscopic indication of an anterior tree.

In preserved material the suprabranchial epithelium is jet-black except for the small patches of white gill tissue, distributed in the " coralline " pattern (see p. 236).

Dinotopterus euryodon (Jackson), 1959

Bathyclarias euryodon Jackson, 1959, *Proc. zool. Soc. Lond.* **132** : 120, fig. 4.

HOLOTYPE. B.M. (N.H.) Reg. No. 1960.2.29.13.

No further specimens have been obtained for study purposes.

SUPRABRANCHIAL ORGAN. In the single specimen (S.L. *c.* 104 cm.) I have been able to dissect, the cavity is not appreciably reduced (length *c.* 28% of head ; volume 107 cc.) but there are no indications of arborescent organs. The gill-fans, on the other hand, are fully developed.

Because the specimen is poorly preserved it was difficult to get a clear histological picture of the suprabranchial epithelium. However, the gill tissue is apparently distributed according to the " Saccobranchus " pattern (see p. 235).

Dinotopterus filicibarbis (Jackson), 1959

Bathyclarias filicibarbis Jackson, 1959, *Proc. zool. Soc. Lond.* **132** : 120, fig. 5.

HOLOTYPE. B.M. (N.H.) Reg. No. 1955.6.14.1 from Nkata Bay.

No further specimens have been collected, but the original description must be emended. In the holotype, at least after preservation, the gill filaments are greyish-black (cf. *D. ilesi* and *D. foveolatus*).

SUPRABRANCHIAL ORGAN. The cavity is long (*c.* 34% of the head) but shallow so that its volume, in the holotype, is 32 c.c. No arborescent organs are visible.

Gill tissue in the suprabranchial epithelium is arranged in the " coralline " pattern (see p. 236); the undifferentiated tissue is jet-black. Identical tissue occurs in *D. foveolatus*.

Dinotopterus worthingtoni (Jackson), 1959

Bathyclarias worthingtoni Jackson, 1959, *Proc. zool. Soc. Lond.* **132** : 123, fig. 6.

HOLOTYPE. B.M. (N.H.) Reg. No. 1960.2.29.18 from Nkata Bay.

No additional study material of this species has been deposited in the Museum. When re-examining the original specimens I found that the gill filaments of the two paratypes (25·4 and 27·5 cm. total length) are greyish-black, except at their extreme distal tips. Neither the small individuals (7·5 and 8·0 cm. S.L.) nor the large holotype (68·2 cm. T.L.) have dark filaments. It seems unlikely that such pronounced darkening of the filaments can be attributed to preservation or to any *post mortem* changes, such as a branchial haemorrhage. If both these explanations are discounted, there remains the suggestion that darkening of the gills can occur as an individual variation. The character might therefore be of reduced taxonomic importance. The gills of *D. ilesi*, *D. foveolatus* and *D. atribranchus* are black in preserved specimens, but as these species are known from very few specimens it is impossible to determine the intraspecific constancy of the character.

SUPRABRANCHIAL ORGAN. The cavity is somewhat reduced (see Table II). Ontogenetic changes in the development of the arborescent organs are clearly seen in these specimens. The trees are greatly reduced at all sizes; no anterior tree is developed, even in the largest fish (the holotype, 68·2 cm. T.L.), and in this fish the posterior tree is represented by a small knob about 3·5 mm. length. In a smaller specimen (23 cm. S.L.) the posterior tree is a weakly trifid knob, proportionately larger than that of the holotype. The smallest fish examined (6·6 cm. S.L.) shows a very early stage in suprabranchial ontogeny, at which no trees are visible and even the " gill-fans " are incomplete.

Gill tissue within the suprabranchial epithelium is distributed in the " Saccobranchus " pattern; no ontogenetic changes in pattern were detected (cf. *D. cunningtoni*, where such changes are found).

Dinotopterus gigas (Jackson), 1959

Bathyclarias gigas Jackson, 1959, *Proc. zool. Soc. Lond.* **132** : 125, fig. 7.

HOLOTYPE. A head and skin B.M. (N.H.) Reg. No. 1960.2.29.35.

Originally based on a single giant specimen 135 cm. S.L., the description must now be modified to include four smaller specimens (one head 28 cm. long and three entire fishes 47·0, 61·0 and 64·5 cm. S.L.).

Length of head contained 2·6–3·6 times in standard length, the dorsal surface smooth and covered with thick skin ; head width 3·9–5·0 in standard length and 1·3–1·4 in head length. Eye diameter 13·7–19·3 in head (showing negative allometry with head length) and 7·2–14·0 in interorbital width (again, negatively allometric). Interorbital width 1·3–1·9 in head, length of snout 3·3–4·3.

Barbels smooth, their length negatively allometric with head length ; nasal barbel 2·7–6·0 in head, maxillary 1·1–2·3, outer mandibular 1·9–3·1, inner mandibular 2·5–4·2.

Premaxillary and vomerine teeth slender and pointed, half length of either band contained about 5 times in head length. Vomerine band continuous or interrupted medially, its width equal to or slightly greater than that of the premaxillary band.

Gill rakers short, 0·5–0·65 of the length of the longest gill filaments ; 100–149 on the first gill arch, the number positively correlated with standard length.

Dorsal fin with *c.* 69 rays, anal with *c.* 56. Caudal peduncle as long as deep or, deeper than long.

SUPRABRANCHIAL ORGAN. The suprabranchial cavity is relatively reduced, particularly in large fishes (see Table II).

In the holotype (S.L. 135 cm.) both arborescent organs are of approximately equal size (an unusual feature but one possibly correlated with the great size of this fish) relatively large and extensively branched. These organs are of disparate sizes (the posterior tree larger) in a head 28 cm. long—estimated to be from a fish *c.* 90 cm. S.L.—and although small in relation to the volume of the cavity are much branched. The same condition is found in a fish 61 cm. S.L. but in a larger specimen (64·5 cm. S.L.) the arborescent organs are reduced to a small, bifid outgrowth on the second arch and a slightly larger, trifid structure on the fourth arch. In the smallest specimen examined (47 cm. S.L.) the anterior tree is represented by a small knob and the posterior tree by a large, sparsely branched outgrowth.

The gill tissue in the suprabranchial epithelium is arranged in the " Clarias " pattern (see p. 235).

Dinotopterus atribranchus sp. nov.

HOLOTYPE. A male, probably adult, 39 cm. S.L. B.M. (N.H.) Reg. No. 1960.2.29.17.

DESCRIPTION. Based on the unique holotype. Length of head 3·5 in standard length, the dorsal surface relatively flattened ; roofing bones rugose, the tubercles arranged in definite patterns. Frontal fontanelle long and narrow, its length 3·7 in head. Width of head 5·2 in standard length and 1·5 in head length. Eye diameter contained 11·2 in head length and 4·8 in interorbital width, which is contained 2·3 times in head length. Length of snout 4·9 in head, distance between anterior nostrils 5·6 times.

Barbels smooth ; length of nasal barbel contained 2·7 times in head length, maxillary 1·4, outer mandibular 2·0 and inner mandibular 3·3 times.

Premaxillary and vomerine teeth fine and pointed, the width of the vomerine band about three-fifths that of the premaxillary.

Gill rakers very short, about 0·3 of the length of the longest gill filament ; 85 on the first gill arch. Gill filaments dark greyish-black.

Dorsal fin with *c.* 60 rays, anal with *c.* 45. Caudal peduncle slightly deeper than long, adipose dorsal very weakly developed.

Vertebrae (excluding the anterior fused mass) 54.

SUPRABRANCHIAL ORGAN. The suprabrancial cavity is reduced, the anterior tree a small stump and the posterior tree a short, six-branched outgrowth. The " gill-fans " are well developed.

Gill tissue in the suprabranchial epithelium is arranged in the " Saccobranchus " pattern (see p. 235).

DISCUSSION. Because this specimen is relatively small it is most likely that the low number of gill rakers is not definitive. On the other hand, the very short rakers may be looked upon as a character unaffected by growth. From Jackson's (1959) analysis of gill raker proportions in *D. nyasensis* and *D. worthingtoni*, and mine of *D. cunningtoni* (below) it is clear that very little change occurs in the relative length of the rakers, even over a wide size range. The gill rakers in *D. atribranchus* are remarkably short even for a species within the group having reduced rakers.

If the possession of black gill filaments is a good specific character (but see p. 227) then *D. atribranchus* is readily distinguished from all other species in the short-rakered group.

The condition of the suprabranchial organs in *D. atribranchus*, even though these probably have not completed their development, distinguishes the species from *D. rotundifrons*, *D. worthingtoni* and *D. euryodon*.

From *D. gigas*, *Dinotopterus atribranchus* is readily distinguished by its rugose skull (at least in the size ranges represented), shorter and narrower snout, and its wider interorbital region.

KEY TO THE SPECIES OF *DINOTOPTERUS*

This key has been built around that produced by Jackson (1959). Like most keys it is unsatisfactory especially since the known range of variation for many of the characters used blurs several of the dichotomies. Two particular points should be noted with care. One is the second dichotomy, based on the number of gill rakers and their relative lengths. I have examined a wide size-range of *Dinotopterus cunningtoni* and find that although the proportional measurement is constant at all sizes, the number of rakers shows a fourteen-fold increase in large fishes (see below). Similar results were obtained by Jackson (op. cit.) for *D. nyasensis* and *D. worthingtoni*.

Gill raker counts and proportional measurements for *D. cunningtoni* :

Head length (cm.)	Length of longest raker / Length of longest filament	Number of rakers
0·7	0·5	12
1·4	0·7	20
1·7	0·7	20
4·7	0·5	55
13·1	0·5	147
16·5	0·7	175
19·3	0·7	200
26·0	0·7	172

From these figures it is clear that the relative length of the rakers is the more reliable " key character "; in larger fishes it is reinforced by the number of rakers.

The second unsatisfactory major dichotomy is the seventh, which is based on the relative length of the maxillary barbels. This measurement is known to show negative allometry with head length, so that small specimens of the species-group alternative to *D. longibarbis* will tend to show the *D. longibarbis* character.

References to the suprabranchial organs and the nature of the suprabranchial epithelium (" Clarias "-like or " Saccobranchus "-like) are discussed fully on pp. 232–7.

I have not used Jackson's character of " black, tarry removable mucus on body " to separate *D. ilesi* from *D. nyasensis* because with preserved material this character is difficult to apply and may be misleading.

1.	Adipose dorsal fin poorly developed or apparently absent	2
	Adipose fin clearly discernible	*D. cunningtoni*
2.	Gill rakers on first arch 0·3–0·6 length of filaments, rarely more than 145 (at least in fishes 7–75 cm. S.L.)	3
	Gill rakers 0·7–1·0 length of filaments, more than 150 (usually 170–260) in specimens > 46 cm. S.L., fewer in smaller fishes	10
3.	Barbels rounded, smooth and simple	4
	Barbels flattened and broad, the maxillary and outer mandibular pair with rounded lappets distally	*D. filicibarbis*
4.	Body smooth, not pitted	5
	Body rough and pitted	*D. foveolatus*
5.	Gills and suprabranchial cavity black	*D. atribranchus*
	Gills and suprabranchial cavity not black	6
6.	Vomerine tooth-band less than 1¼ times as broad as the premaxillary band; teeth fine, discrete and pointed	7
	Vomerine tooth-band more than 1½ times broader than the premaxillary band, teeth coarse and blunt	*D. euryodon*
7.	Maxillary barbel not reaching beyond the tip of the pectoral fin	8
	Maxillary barbel reaching well beyond extremity of pectoral fin	*D. longibarbis*
8.	Snout length contained less than 4·6 times in head length; dorsal outline of snout slightly curved; head not noticeably chubby	9
	Snout at least 5 in head, rounded. Head chubby	*D. rotundifrons*
9.	Base of maxillary barbel markedly conical, swollen and fleshy. Suprabranchial trees greatly reduced; only a small stump with 4 or fewer branches on the fourth gill arch, at least in fishes > 20 cm. S.L., absent in fishes, < 7 cm. S.L.	*D. worthingtoni*
	Base of maxillary barbel not markedly enlarged. Arborescent suprabranchial organs on second and fourth gill arches, at least in fishes > 45 cm. S.L., much branched in large fishes, sparsely branched in specimens 45–60 cm. S.L.	*D. gigas*
10.	Body relatively slender; maxillary barbel (at least in fishes 27–69 cm. S.L.) contained 1·8–2·2 in head	11
	Body stout; maxillary barbel 1·2–1·7 in head	12
11.	Gill filaments and epithelium of suprabranchial cavity purplish-black	*D. ilesi*
	Gill filaments and epithelium of suprabranchial cavity colourless in preserved specimens	*D. nyasensis*
12.	Suprabranchial arborescent organs merely a simple stub on the 4th gill arch; suprabranchial epithelium of the " Saccobranchus " type. Dorsal surface of head with few rugosities	*D. jacksoni*

Suprabranchial arborescent organs moderately well developed on 2nd and 4th arches, much branched in specimens 50–80 cm. S.L. (but reduced to a small four-branched tree on the fourth arch in a fish 20 cm. S.L.) ; suprabranchial epithelium of the " Clarias " type . . . . *D. loweae*

THE SUPRABRANCHIAL RESPIRATORY ORGANS IN THE CLARIIDAE

Several descriptions of the suprabranchial organs have been published since the original but remarkably complete account of their anatomy given by E. Geoffroy St. Hilaire in 1802. This author's preliminary notes (published by Lacepède, 1836) describing the appearance of the organs and their probable respiratory function, still provide one of the most succinct accounts available.

Of the more recent papers, that of Rauther (1910), giving a detailed histological account, and that of Marlier (1938), providing a more general description, are the most comprehensive.

Variation in the suprabranchial region of the Clariidae is considerable (see below and also David, op. cit.: Poll, 1942 ; Greenwood, 1956 and 1959) but in the majority of species the following brief description is applicable.

Above the gill chamber there is a spacious cavity, enlarged posteriorly where it extends ventrally to about the level of the pharyngeal floor. The lateral floor and walls of the cavity are formed by certain modified and membraneously united, fan-like gill filaments on the upper part of each gill arch (hereafter referred to as the " gill-fans "). The entire chamber, excluding the fans, is lined with highly vascularized epithelium irrigated by afferent and efferent blood vessess from each gill arch. As might be expected, the " gill-fans " have the histological structure of gill filaments. A similar histology is shown by the epithelium lining the cavity (Rauther, op. cit. and personal observations).

Thus, as Carter (1957) emphasized with regard to the arborescent organs in *Clarias* (see below), the respiratory epithelium is not merely a direct modification of an unmodified internal surface. It is, in fact, a modification and extension of the normal branchial tissues. What at first sight appears to be the differentiation of typical gill tissue within unmodified epithelium during the ontogeny of the suprabranchial cavity (see below, p. 235), can be interpreted in a different way. The spatial relationships of the tissue to the gills is extremely intimate as is clearly seen in the embryo. This tissue could, therefore be considered as primarily branchial ; if this is so, the relatively late appearance of gill cells could be interpreted as the delayed manifestation of its competence to develop into branchial tissue.

Contained within the cavity and occupying up to four-fifths of its volume are two much-branched arborescent structures (the " trees ") developed from the epibranchials of the second and fourth gill arches. The epithelium covering the cartilaginous skeleton of each tree has the histological structure of gill tissue. It is supplied with afferent and efferent blood vessels from the corresponding gill arch.

In every *Clarias* species investigated the size and complexity of the arborescent organs are positively correlated with the size of the individual and, of course, with its ontogenetic stage. I have studied the complete ontogeny of the suprabranchial organs in *Clarias mossambicus* and the following notes summarize my observations. For comparative purposes it should be noted that the modal adult size-range of *C. mossambicus* in Lake Victoria is 50–90 cm.

The arborescent organs develop late in post-larval ontogeny (Greenwood, 1956); a single knob associated with the fourth arch appears in fishes of *c.* 3 cm. length. The anterior tree (second arch) develops somewhat later. When the fish is about 5 cm. long, the posterior tree is trifid; branching then continues until the much-branched definitive condition is attained when the fish is about 30 cm. long. Development of the anterior tree follows a similar pattern but always lags behind that of the posterior one; ultimately it is about two-thirds the size of the latter. When fully developed, the two trees occupy 70–80% of the suprabranchial cavity.

Differentiation of gill tissue within the suprabranchial epithelium occurs before the appearance of the trees; suprabranchial lamellae first appear when the fish is about 1 cm. long.

The "gill-fans" are the last suprabranchial structures to develop and usually complete their differentiation from the gill filaments only after the macroscopic appearance of the posterior tree. Obvious morphological changes are, however, apparent in those filaments destined to form the "fans" at about the time of the first appearance of lamellae in the lining epithelium. Until the "fans" are fully developed, the suprabranchial cavity has wide openings into the branchial and pharyngeal cavities. The cavity must, therefore, be filled with water and in early post-larval fishes probably acts as an aquatic gill. Hora (1935) has shown that the lung-like air-sacs of *Amphipnous* can be utilized in this way.

Suprabranchial respiratory organs are not well developed in all Clariidae and in some genera may be entirely absent. With one exception (the genus *Dinotopterus*), clariids with greatly reduced organs are small. Various stages in suprabranchial reduction are manifest by these genera and also in some of the smaller *Clarias* species (those belonging to David's subgenera *Clarias* (*Clarias*) and *C.* (*Allabenchelys*)).

THE SUPRABRANCHIAL ORGAN IN *DINOTOPTERUS*

Perhaps the most outstanding anatomical feature of the Lake Nyasa *Dinotopterus* species is the wide interspecific variation in the suprabranchial organ. Differences are most evident in the morphology of the arborescent organs but also appear in the histology of the suprabranchial lining epithelium. No other clariid genus shows such variation; I have examined seventeen *Clarias* species and found that, within any one of the three subgeneric groups, the degree of suprabranchial organization and development is remarkably constant. *Dinotopterus* stands in sharp contrast. Here one finds within a single species-flock some species in which both trees are present and fully developed, others with small, sparsely branched trees and finally, a large group of species in which no anterior tree is developed and the posterior tree is greatly reduced or even absent (see Table I). When polyfid arborescent organs are present, as in large *D. ilesi* and *D. gigas*, the trees are relatively reduced and occupy a smaller volume of the cavity than do the trees of adult *Clarias mossambicus* and other members of the *C.* (*Heterobranchoides*) subgroup. Such trees in *Dinotop-*

TABLE I.—*Types of Arborescent Organs and Suprabranchial Epithelium in* Dinotopterus *Species*

(1) Arborescent organs present, relatively large and much branched	Suprabranchial epithelium*	(2) Arborescent organs present, small and sparsely branched	Suprabranchial epithelium*	(3) Arborescent organs absent or represented by a stub on 4th arch	Suprabranchial epithelium*
Dinotopterus ilesi	Sb.	*Dinotopterus nyasensis*	Sb.	*Dinotopterus filicibarbis*	cor.
Dinotopterus loweae	Clar.	*Dinotopterus atribranchus*	Sb.	*Dinotopterus euryodon*	cor.
Dinotopterus longibarbis	Clar.			*Dinotopterus cunningtoni*	cor.
Dinotopterus gigas	Clar.			*Dinotopterus worthingtoni*	Sb.
				Dinotopterus rotundifrons	cor.
				Dinotopterus jacksoni	Sb.
				Dinotopterus foveolatus	cor.

* Clar. = "Clarias"-type. Sb. = "Saccobranchus"-type. cor. = "coralline"

TABLE II.—*Data on the Gill Area, Volume of the Suprabranchial Cavity and the Number of Filaments on the First Gill Arch of Certain* Clarias *Species Compared with those of* Dinotopterus *Species*

Clarias§	Head length (cm.)	"G.A"*	Sbr.† vol. (c.c.)	Fil.‡	*Dinotopterus* (1) and (2)	H.L. (cm.)	"G.A."	Sbr. vol. (c.c.)	Fil.	*Dinotopterus* (3)	H.L.	"G.A."	Sbr. vol. (c.c.)	Fil.
C. mossambicus	11·5	191	12	80	*D. ilesi*	18·2	1,556	25	—	*D. filicibarbis*	21·0	2,580	32	175
	18·0	601	—	—		20·0	1,858	54	—	*D. euryodon*	13·7	947	—	—
	18·8	638	58	110		20·5	1,714	56	—		29·0	4,443	*c.* 107	—
	25·5	961	—	115	*D. loweae*	14·7	813	14	—	*D. cunningtoni*	13·3	1,243	4·4	176
						19·8	1,660	80	—		26·0	5,641	31	—
C. lazera	15·7	414	21	100		23·2	3,081	84	—	*D. worthingtoni*	6·3	119	—	—
	24·8	708	151	100		26·3	3,560	60	—		6·5	117	1	—
					D. longibarbis	16·5	1,230	57	120		19·6	1,638	36	—
C. mellandi	11·0	217	11	—		22·0	—	—	150	*D. rotundifrons*	15·0	1,360	3	—
					D. gigas	19·5	1,533	32	170		15·7	1,698	—	—
						21·7	2,830	43	—					
						28·0	5,324	—	—	*D. jacksoni*	20·5	2,319	24	180
											21·8	3,347	21	—
					D. nyasensis	9·4	353	3	144		23·0	2,745	43	—
						16·2	1,481	16	190					
						19·7	2,022	38	174					
										D. foveolatus	12·6	645	2	123
					D. atribranchus	11·1	603	2	—		15·0	1,228	—	148

The species of *Dinotopterus* are grouped in two major classes corresponding to the type of arborescent organ developed. The first class corresponds to groups 1 and 2 of Table I, the second to group 3.

* "Gill-area"; see text, p. 238.
† Volume of suprabranchial cavity (arborescent organs removed if developed).
‡ Number of filaments on the first gill-arch.
§ All species with hypertrophied arborescent organs.

terus bear the same relationship to those of *C.* (*Heterobranchoides*) species as do the reduced arborescent organs found in the subgroup *Clarias* (*Allabenchelys*), (see David, op. cit.).

Interspecific variation in the volume of the suprabranchial cavity is moderately high, but only four species have an obviously shallow chamber (see Table II). In all *Dinotopterus* species the " gill-fans " are fully developed.

Interspecific variability is not confined to gross structures but also occurs in the histology of the epithelium lining the cavity. Indeed, apparently novel arrangements of certain tissues are found in some *Dinotopterus* species, although it should be remembered that this aspect of the suprabranchial organ has not been studied at all intensively.

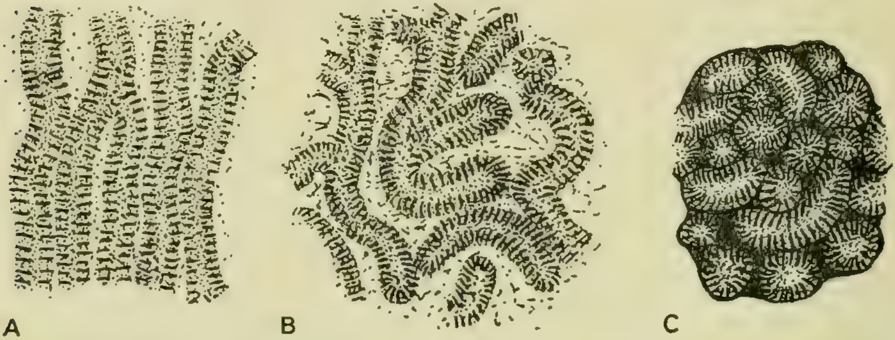

FIG. 1. Fragments of suprabranchial lining epithelium seen in surface view, showing the three types of lamellar organization. A. " Clarias "-type ; B. " Saccobranchus "-type ; C. " coralline "-type. Magnification *c.* 50×.

Reference should be made to Rauther (1910) for a full and well-illustrated account of the histology of the suprabranchials in the Clariidae. As this author demonstrated, the epithelium lining the suprabranchial cavity of *Clarias* and the air chamber of *Saccobranchus* (= *Heteropneustes*) is differentiated into branchial and non-branchial tissue. The branchial tissue, which is arranged along the numerous blood-vessels, has the histological structure of normal gill-lamellae, save for the absence of gill rays. In the *Clarias* which I have examined (*C. mellandi*, *C. mossambicus*, *C. carsoni*, *C. pachynema*, *C. salae*, *C. jaensis*, *C. hilgendorfi* and *C. dumerili*) the suprabranchial lamellae are arranged in a basically linear but gently sinuous fashion (see Text-fig. 1A). This distribution of suprabranchial lamellae I have named the " Clarias " type or pattern. A second pattern is that found in the air-sac of *Heteropneustes* (see Rauther, op. cit., fig. 22). Here, the linear arrangement is obscured by the extreme sinuosity of the lamellae. A very similar pattern occurs in the suprabranchial epithelium of several *Dinotopterus* species (see Text-fig. 1B, and Table I) ; it differs slightly from the *Heteropneustes* type inasmuch as the lamellae are shorter and more irregularly arranged. This type of tissue occurring in *Dinotopterus* I have called the " Saccobranchus " type.

Yet a third pattern is found in *Dinotopterus*. In this type (the " coralline "), many lamellae have, as it were, contracted and formed small, circular or ovoid patches of gill tissue interspersed amongst the less numerous patches of elongate lamellae. In contrast to the " Saccobranchus " type, there is much less inter-lamellar tissue in the " coralline " type of epithelium (see Text-fig. 1C). A further peculiarity in two of the five species with " coralline " epithelium is the heavy concentration of melanin deposited in the inter-lamellar tissue. As a result, the suprabranchial chamber is black except for the patches of gill tissue. Some melanin is found between the lamellae in other species but in none does it reach sufficient density to colour the epithelium.

Taking the " Clarias " pattern as basic, a comparison of the three types of suprabranchial epithelium suggests that the others could have evolved by a process of folding and fragmentation of the originally linear lamellae. Evidence from *D. cunningtoni* (see p. 220) seems to support this idea, at least for ontogeny.

Correlating the type of suprabranchial epithelium with the type of arborescent organ present, shows that (i) The " Clarias " type only occurs in species in which both trees are present and well- or moderately well-developed. (ii) Species without trees or with mere stumps on the fourth arch have either the " Saccobranchus " or " coralline " types of epithelium. (iii) The " Saccobranchus " pattern also occurs in species with well- or poorly-developed trees (see Table I). No adaptive value for any particular type of epithelium is immediately suggested by this analysis. That question is unlikely to be answered until we know more about the physiological significance of the suprabranchial organ in these essentially deep-water species.

When compared with the definitive condition in *Clarias*, the suprabranchial region in *Dinotopterus* shows a wide range of developmental types. The question then arises: are these stages representative of a regressional or a developmental phase ? This question is not readily answered but must be considered.

Evidence from comparative anatomy and ontogeny is somewhat equivocal but, I believe, suggestive of regression from the *Clarias* and *Heterobranchus* condition. *Dinotopterus* is most closely related to *Clarias* and, more distantly, to *Heterobranchus*. In both these genera the suprabranchial organ is complete and well-developed, at least in adult and near-adult fishes. Species of both genera are virtually restricted to shallow waters of lakes, rivers and certain types of swamp. By inference from experiments made on several *Clarias* species (see below), the species are dependent on the suprabranchial structures as aerial respiratory organs; purely aquatic respiration is insufficient to fulfill their respiratory requirements. Species of *Dinotopterus* on the other hand, are characteristic of deep-water habitats although some have a wide vertical range, which includes the pelagic as well as benthic zones (Jackson, 1959). For fishes living at depths of 40–70 metres, dependence on aerial respiration would be a severe handicap. Indeed it would probably prevent the invasion of these depths. Since the original fish-fauna of Africa would be essentially one of rivers and swamps, it seems that the trend in *Dinotopterus* is one leading away from an adaptation to such habitats and towards a bathypelagic and benthic existence. Deep-water habitats can be looked upon as relatively " youthful " because the East and Central African lakes are geologically young features, certainly post-dating the primary distribution of freshwater fishes over the continent.

A second indirect approach to this problem is afforded by the vertical distribution of the Nyasa species. No general correlation exists between the type of suprabranchial organ and the depths at which the species occur. Thus, and rather unexpectedly when compared with *Clarias*, at least one pelagic and one partly pelagic *Dinotopterus* species is without arborescent organs; in contrast, one deep-water species (*D. gigas*) has well-developed trees. Furthermore, developed trees are found in three species whose range extends from the pelagic zone down to a depth of 50 metres. These data strongly suggest that the species involved have broken away from the obligatory aerial respiration which restricts the vertical distribution of *Clarias* and *Heterobranchus* to shallow water. Once this physiological step has been taken, the stage is set for the regression of organs primarily concerned with air-breathing. It is interesting to note that three species found at the greatest depths. and which have not been recorded from the pelagic region (*D. foveolatus*, *D. filicibarbis* and *D. rotundifrons*), are all without arborescent organs and the volume of the suprabranchial cavity is greatly reduced.

The means whereby this breakaway from obligatory air-breathing was achieved, is discussed below.

PROBABLE METHODS OF RESPIRATORY COMPENSATION IN *DINOTOPTERUS*

Many experiments on several *Clarias* species (Boake, 1865; Das, 1927; and personal observations) all indicate that the suprabranchial organs are essential for life in this genus, the nearest living relative of *Dinotopterus*. Even in well-aerated water *Clarias* are apparently incapable of sustaining themselves by purely aquatic respiration. Hora (1935) is the only worker to claim that *Clarias* is not asphyxiated if it is kept in well-aerated water. Unfortunately, none of the authors investigating this phenomenon has cited the actual oxygen tensions of the water in which the fishes were kept. Personal field observations on *Clarias mossambicus* in Lake Victoria strongly suggest that even in the well-oxygenated waters of the Lake (O_2 concentrations 6–7 p.p.m.; 85–100% saturation) larger individuals (*c.* 50–80 cm. long) are forced to utilize their aerial respiratory organs. From this, I can only conclude that if purely aquatic respiration is possible, then the water would have to be oxygenated to an extent not generally encountered in the usual habitats of the species.

No *Dinotopterus* species has such well-developed suprabranchial arborescent organs as are found in *C. mossambicus* nor is there any indication that the oxygen concentrations occurring in Lake Nyasa are much greater than 7 p.p.m. (Beauchamp, 1953). Furthermore the depths at which most species occur is such that it seems impossible for the species to utilize the organs for surface air-breathing.

Some compensatory device is clearly involved and, as would be expected, this involves an increase in the surface area of the gills. The gills in all *Dinotopterus* species are considerably larger than those of equivalent sized *Clarias* (see Table II). The increase in area has been achieved both by elongation of the filaments and an increase in the number of filaments per arch. In large specimens there are about

50–70% more filaments on the first arch than in a comparably sized *Clarias*. As far as I could determine, the number of lamellae per millimetre of filament is approximately the same in large fishes of both genera.

The data given in Table II are admittedly crude but nevertheless clearly show intergeneric differences in gill size as well as interspecific differences within *Dinotopterus*. As a basis for size comparison I have chosen head length, principally because most of the larger *Clarias* material is of heads only. The character " gill area " was measured by tracing the outline of the filamentous part of the first gill arch (excluding the " gill-fans ") onto squared paper divided into millimetre units. The results, therefore, by no means reflect the true surface area of the gill, but are merely a convenient way of indicating the size differences in this gill. It is obvious that with these crude measurements the figures obtained cannot be compared with the exact measurements given by Gray (1945) or Saxena (1958) for the gill areas of various marine and freshwater fishes.

The volume of the suprabranchial cavity was measured by filling the chamber with fine lead-shot ; in those species (particularly *Clarias*) with expansive arborescent organs, the organs were removed before determining the volume.

Data in Table II show not only the remarkably larger gills of *Dinotopterus* but also several points in connection with the volume of the suprabranchial cavity, its correlation with gill area and its relationship to head size in the different species.

With so few specimens it is difficult to generalize on intraspecific variation in the volume of the cavity, which may be greater than appears from these figures. In the *Clarias* species studied, the suprabranchial cavity is large and becomes relatively larger with the growth of the individual. This allometric relationship is also shown by all species of *Dinotopterus*. In two species (*D. ilesi* and *D. loweae*) the volume of the cavity is equivalent to that of *Clarias mossambicus* and *C. lazera*, at least in fishes with a head length of 14–20 cm.; but in larger *D. loweae* (H.L. 23–26 cm.) the cavity is relatively smaller. Only one species, *D. longibarbis* (represented by a single specimen), has a suprabranchial cavity relatively larger than that of *Clarias*. All other *Dinotopterus* species have the cavity smaller than in *Clarias* and in some (*D. foveolatus*, *D. rotundifrons* and *D. cunningtoni*) very considerably smaller both in relation to *Clarias* and to other *Dinotopterus* species.

With one exception, in all the *Dinotopterus* species compared there is a weak inverse correlation between " gill area " and cavity volume ; even species within the group having the most reduced cavities show this relationship.

The functional significance of the suprabranchial cavity in *Dinotopterus* has not been investigated. That the cavity is highly vascular and predominantly branchial in its histology, strongly suggests that it serves some respiratory function. Jackson (1959) reports sighting several species feeding at the surface. In these species and under such circumstances, the suprabranchial organ may still function as a means of aerial respiration. But the vertical range of the same species also extends to the deep water and there are those species which apparently never leave the depths. Under such circumstances, the suprabranchial epithelium may serve as an aquatic respiratory surface. Hora (op. cit.) has shown that, if emptied of air, the aerial respiratory organs of *Ophiocephalus*, *Anabas* and *Amphipnous* can serve as gills.

It is, of course, essential that the cavities be largely emptied of air and I can see no reason to believe that this could not happen in *Dinotopterus*, especially when the fish is subjected to pressure. The valve system formed by the " gill-fans " is not particularly muscular and water under pressure should easily flood the suprabranchial chamber. The shape of the cavity and the arrangement of the valves are such that little or no air could remain trapped in it.

The four species with the proportionately smallest suprabranchial cavities (*D. filicibarbis*, *D. rotundifrons*, *D. foveolatus* and *D. cunningtoni*) all have suprabranchial epithelium of the " coralline " type. The significance of the relationship has still to be determined. The only other species with " coralline " epithelium is *D. euryodon* but here the cavity is relatively large. Altogether there is little correlation between tissue-type and cavity size, except the negative one that " Clarias "-type epithelium is not found in species with a reduced chamber and tends to be associated with large arborescent organs. " Saccobranchus "-type tissue, on the other hand, occurs in both large and small chambered species but is commonest in the group of species which have reduced arborescent organs or are without these structures.

SUPRABRANCHIAL REGRESSION IN OTHER CLARIIDAE AND A COMPARISON WITH *DINOTOPTERUS*

The regressional series represented in descending order of suprabranchial organization by the genera and subgenera *Heterobranchus*, *Clarias* (*Heterobranchoides*), *C.* (*Clarias*), *C.* (*Allabenchelys*), *Chanallabes*, *Clariallabes*, *Gymnallabes* and *Tanganikallabes* (the organ is absent in *G. thioni* and *T. mortiauxi*) is well known and need not be elaborated upon here (David, op. cit.; Marlier, op. cit.; Poll, 1942*b* ; Greenwood, 1956). Three points, however, should be noted ; first, the series shows an overall decrease in maximum size ; second, the body becomes increasingly anguilliform and third, the trend also involves the regression of certain roofing bones in the skull. Indeed, this series has been interpreted as an example of evolution through neoteny (Poll, 1942*b* ; Greenwood, 1956).

Another unrelated example of suprabranchial regression is provided by the genus *Xenoclarias*, at present known from two deep-water species in Lake Victoria (Greenwood, 1958). In this genus, there is no suprabranchial cavity, no arborescent organs and the " gill-fans " do not develop. Instead, the upper filaments of each gill arch retain their filamentous nature. Unlike the more regressed members of the *Clarias* → *Tanganikallabes* line, *Xenoclarias* does not show any neotenic characters. Apart from its peculiar branchial arrangements it is a typical member of the subgenus *Clarias* (*Clarias*), although its adult size is small (15–16 cm. S.L.).

As David (op. cit.) first pointed out, the small size of fishes with regressed suprabranchials would enhance the possibility of cutaneous respiration and thus provide some compensation for the loss of the aerial respiratory organs. In *Xenoclarias*, besides increased surface area relative to volume there is an increase in gill surface because the " gill-fans " are suppressed.

The species of *Dinotopterus* provide yet another line of suprabranchial regression which differs in certain respects from the other two. An outstanding difference is the large adult size of all *Dinotopterus* species, amongst which are to be found some of the largest Clariidae. Clearly, increased cutaneous respiration is not a compensating respiratory mechanism in these fishes ; increased gill area, however, seems to be the factor involved (see p. 237 and Table II).

The state of the suprabranchial organ in a few of the less regressive *Dinotopterus* (group 1 in Table I) is comparable with that of certain *Clarias* (*Allabenchelys*) *dumerili*; other species of this subgenus, the most regressive of the *Clarias*, have arborescent organs relatively larger and more complex than *Dinotopterus*. I have found regressed arborescent organs in only one population of *Cl.* (*A.*) *dumerili*, that occurring in the Cuvo River, Mount Maco, Angola. Other populations of this species have arborescent organs typical of the subgenus, of which the following species were dissected : *C. carsoni*, *C. submarginatus*, *C. philipsi*, *C. longior*, *C. poensis*, *Allabenchelys longicauda* and *All. brevior*). Likewise, the relative development of the suprabranchial organ in *Chanallabes* species is greater than in *Dinotopterus*. In certain respects, namely the absence of arborescent organs and a decrease in the volume of the cavity, the suprabranchials of *Clariallabes petricola* and *Dolichallabes microphthalmus* compare with the majority of *Dinotopterus* species ; in *Cl. petricola*, however, the " gill-fans " are less developed. The only clariid species which seem to show regression in the suprabranchials even greater than that of *Dinotopterus* are *Gymnallabes thioni* and *Tanganikallabes mortiauxi* (see Poll, 1942*a* ; 1953).

CONCLUSION

Regression of the suprabranchial respiratory organs has been achieved in many species of Clariidae. The manner of their decline and the provision of compensatory means of respiration show considerable variation, but all seem to involve heterochronic growth either affecting the organs alone or the entire skull. Species with reduced suprabranchials are found in a great variety of habitats including swamps, fast flowing rivers and the deep waters of lakes. Those species with elongate bodies have even invaded such habitats as the interstices of rocks and coarse gravel on river beds. As a group the " regressive " clariids have probably proved more successful (as measured by variety of habitat) than those species and genera which have retained a fully-developed suprabranchial organ and the concomitant obligatory air-breathing habit. Geographically, however, their distribution is limited to the approximate area of 5° N. to 15° S. as compared with the almost pan-African and Asiatic distribution of the fully air-breathing species (see David, op. cit.).

This study has not thrown much more light on the evolution of air-breathing organs in the Clariidae. However, from what has been said it is clear that I support Beadle's (1932) views on the environmental conditions favouring the origin and development of such structures. Beadle supposed that aerial respiration was of considerable adaptive value to fishes living in near-stagnant and poorly oxygenated closed swamps. That is, swamps not connected with open water as are most present-day African swamps. He further supposed that closed swamps probably preceded the formation of the open type. The geological history of most African lakes certainly supports this interpretation of geomorphological events. Thus, invasion of open-water habitats would perforce take place at a later date and after the fishes had evolved an accessory aerial respiratory mechanism.

When reviewing Beadle's ideas, David (op. cit.) doubted this sequence of events, particularly since there is the implication in Beadle's paper that in open lake conditions, the suprabranchial respiratory organs would be redundant. As David comments, the highly developed accessory respiratory organs of *Heterobranchus* and *Clarias* hardly have the appearance of " Reliktorgane ". But, from what we know of the respiratory requirements of *Clarias* this is literally what these structures are, organs developed in a different environment but now forming an integral part of the animal's physiology no matter what environment it may occupy. This interpretation of the suprabranchial organs in *Clarias* and *Heterobranchus* seems to answer David's objection and to link the ideas of both this author and Beadle. A truly regressive accessory respiratory organ is only seen, so I believe, in those Clariidae which have developed some compensatory respiratory mechanism (such as increased cutaneous respiration through decreased body-size, or enlargement of the gill area). With regard to these organs, the Clariidae as a whole may be an example of cyclic evolution. That is to say there has been the primary evolution of an aerial respiratory organ to meet the challenge of a severely deoxygenated environment and then, in certain branches, the loss of these structures when a new set of moderately well-oxygenated habitats were themselves evolved and were available for exploitation.

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THE TAXONOMY AND IDENTIFICATION OF PIPITS
(genus Anthus)

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NATURAL HISTORY

B. P. HALL

12 APR 1961
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By B. P. HALL

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INTRODUCTION

THE difficulties of distinguishing the different species of pipit, both in the hand and in the field, are well known. While the standard handbooks for different countries deal with identification of the various forms in their own areas, little attempt has been made to define the characters and relationships throughout the world. Unfortunately lack of adequate field experience of pipits precludes me from discussing this aspect, but the collection of over 2,000 skins in the British Museum, supplemented by loans of critical specimens from elsewhere, has enabled me to study all species in the hand, with particular emphasis on those Old World species that present most difficulty in recognition. From that study this paper has been compiled in order to help others to identify pipits and to understand better the relationship between the different species.

The first part deals with an analysis of the diagnostic usefulness and limitations of five important characters—colour and pattern (with particular reference to changes caused by moult and wear), size, conformation of the hind claw, tail pattern, and wing formula. These characters have been selected for specific identification, though this does not imply that there are no others. In identifying the majority of pipits all five should be used in conjunction, and the evidence of the eye in respect of colour and pattern should be backed by measurements and comparison of tails, wings and claws. Since no one character is wholly diagnostic, and all are liable to occasional misinterpretation, no " Key to Species " has been made, for doubt and error would always be liable to intrude in its use. Furthermore, it is inevitable in any key that more stress is laid on the characters first used to subdivide a group than on subsequent characters, which gives them an exaggerated importance. I find it impossible also to subdivide the genus on a systematic basis without over-stressing the importance of one or other character, and propose instead to divide it into three groups which may facilitate identification.

Group A includes fourteen species of Old World and Australasian pipits all of which have a typical pipit-like appearance and a wide range, and therefore present most problems in identification. The measurements of all species in this group are listed together in Table 2–9 for easy comparison and all are illustrated by photographs and by sketches of their tail patterns, wing tips and hind claws. Any typical Old World pipit should be compared with these plates and then checked with the text and the tables of measurement.

Group B comprises two Asian, eight African and one Australasian species which, through some distinctive feature in colour, pattern or size, are unlike the typical pipits of Group A. Most of them have a restricted distribution and offer few problems of identification to anyone with the appropriate regional handbook. They are not illustrated but their characters are outlined under the same formula as is used in Group A for easy comparison, with a final summary of their distinctive features.

Group C comprises ten exclusively American or South Atlantic species. Lack of extensive material has prevented these being studied as fully as the Old World pipits, but they also have their characters outlined as in Group B

While this study is chiefly concerned with specific characters, subspecific variation cannot wholly be ignored and therefore some of the difficulties of subspecific definition and recognition have been discussed. Under each species geographical variation is outlined but the ranges and characters of individual races are defined only when they are relevant to the discussion, or in the few cases in which I disagree with currently accepted views.

Since this paper was completed Volume 9 of the *Check-List of Birds of the World* has been published. This contains the systematic list of the family Motacillidae with full references to all subspecies and to many names considered synonyms. It seems therefore superfluous to list these again here, but I have listed in the Appendix all amendments proposed in this paper to that systematic list.

THE DIAGNOSTIC USEFULNESS AND LIMITATIONS OF CERTAIN CHARACTERS

Colour and Pattern, and the Effects of Moult and Wear

In appearance the majority of pipits vary only in the basic shade of brown above, the whiteness or buffiness below, and in the degree of streaking above and below. Furthermore, since pipits have a soft plumage, noticeably softer for instance than that of larks, and many spend much of their time on the ground or in grass, there is considerable seasonal wear as a result of which some differences of colour and pattern become lost. To off-set this wear and abrasion many species have a partial or a complete spring moult which may, or may not, be into a distinctive breeding dress. The completeness of this moult may vary within populations of the same species as Mayaud (1952) has shown in his study of the European Rock Pipits ; in these the apparent differences between the spring plumages of the Scandinavian and British populations are due to the former having a more complete moult.

It is not generally appreciated that some other species have a haphazard partial moult during the winter months, of body feathers, rectrices, innermost secondaries, wing coverts and, occasionally, primaries. This moult has been observed in Richard's Pipit, *A. novaeseelandiae*, the Tawny Pipit, *A. campestris*, and Blyth's Pipit, *A. godlewskii* ; it has been studied chiefly in the migrant Asiatic races of Richard's Pipit (*A. n. richardi* subspp.) for in these races the breeding season is limited to a few weeks in mid-summer and it is therefore possible to limit the date of post-breeding moult within a short period. Moreover there are abundant winter specimens of this pipit available. An analysis of the moults in two hundred and sixty-eight specimens collected from October to May shows that moult in the primaries is more prevalent in birds which reach furthest south, the examples examined, being from Ceylon (5 specimens), Andaman Islands (2), Madras (1), Siam (3), Laos (1), and Bengal (1 on migration, 24th April). This suggests that the moult has a functional usefulness in replacing worn feathers prior to a long journey and may be developing in the course of evolution as an efficient character increasing the survival chances. Where there is moult in the primaries it is symmetrical in both wings, complete and in sequence, but otherwise there seems no regular sequence to the winter moult : in different specimens central rectrices have been found coming in before, after, and concurrently with other rectrices : moult may be found in body, wings and tail alone, or in all three together, or in any two alone.

Post-breeding moult in *A. n. richardi* subspp. takes place in July and August, or early September at the latest : I have found no indication that it is other than a normal complete moult. The following table (Table I) shows the percentage of specimens examined in which moult in different parts of the body is taking place in the winter ; it suggests that, in some birds, some feathers may be moulted three times a year, and there are three peak moulting seasons, in July, December and March–April.

These figures are based only on specimens in which actual feathers in sheath have been found. As these feathers are frequently lost in skinning the number of specimens in moult at the time of collecting is probably higher than indicated.

TABLE I.—*Haphazard Winter Moult in* A. n. richardi *subspp.* (% *to nearest whole*)

	Month							
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apl.	May
Number of specimens . . .	23	33	39	44	39	31	29	30
Moult of body, wing-coverts or secondaries	21%	57%	66%	36%	35%	87 %	89%	53%
Moult of central rectrices . .	17%	12%	28%	7%	18%	45 %	14%	—
Moult of other rectrices . . .	8%	8%	10%	2%	7%	29 %	20%	10%
Moult of primaries	10%	—	6%	2%	2%	16 %	14%	—
Total showing moult in some part, or parts	35%	57%	72%	38%	41%	87%	89%	53%

It will be appreciated therefore from the examples of the Rock Pipit and Richard's Pipit how important an understanding of moult can be in making comparisons of colour and pattern in pipits, and only birds collected in the same month and in the same condition of plumage should be used. In all species of Group A I have indicated where possible what moults are to be expected but in many species of Groups B and C too few specimens are available on which to generalize, and too little is known of the breeding seasons.

In describing the plumages it is difficult to express some of the differences in colour and pattern. For the basic colour of the upper parts I have used the term " tawny brown " to indicated a light, sandy shade such as is characteristic of the Tawny Pipit, *A. campestris* ; " light brown " for a less sandy tone ; " olive-brown " for a greener brown ; and " dark brown " or " chocolate " for the darker tones ; but these terms, must, inevitably, cover a wide range of individual variation.

In defining the amount of pattern on the breast I have used the terms " streaking " and " spotting " to differentiate between the species which have true streaks and those which, like *A. novaeseelandiae,* have the streaks reduced to small triangular marks.

The term ' scalloping " has been used for the effect caused by white or light edges to the mantle feathers, which is found in some young birds.

Size and Measurements

The uniformity in size among pipit species enhances the value of small differences in proportions, and the usefulness of detailed measurements is readily apparent in the various tables that have been compiled : this usefulness, unfortunately, is limited to a large extent by human inconsistency in measuring, particularly in the dried skin. This does not apply to wing measurements of small birds like pipits in which little or no variation will be found between the figures arrived at by two careful measurers on the same series. I believe, however, that the range of wing measurements for any form based on a series of skins, will always be found to be a trifle smaller than the range based on live birds handled in ringing, due to some shrinkage of the wing in drying. Tails, in the dried skin, present a greater difficulty and an experiment carried out with four experienced measurers, on tails between 60 and 80 mm., showed a degree of variation up to 5 mm., due wholly to the degree of pressure exerted in fitting the tip of the dividers into the angle where the central rectrices join. On a re-trial each measurer was found to obtain consistent results in his or her technique. This individual variability obviously detracts from the value of published tail measurements but they have been included since specimens measured by the same hand are useful comparatively and the variation is limited. However it should be borne in mind when consulting the table that I am among those who give shorter measurements than some others. There is a further difficulty with the wings and tails of pipits for, due to wear, the feathers are rarely wholly perfect especially among birds that are on their breeding grounds. Since it is only these birds that are useful in studying geographical variations they must be used but some judgment is needed to determine which are too worn for inclusion in measurement tables.

Bill measurements made with different quality dividers may show a difference of 0·5 mm. : all quoted in this paper have been taken from the base of the skull using a fine-pointed pair. Tarsus measurements are dependent on the make-up of the skins but the degree of possible error is limited.

These difficulties are stressed here since it is important that the "Tables of Measurements" shall be used with discretion and understanding for identification.

Conformation of the Hind Claw

The length and shape of the hind claw is one of the most reliable aids to specific identification but the limitations must also be understood. Firstly there is in all species some individual variation in length and curvature, which is indicated in the text by the measurements for each form and in the species figured. To this is added some geographical variation, particularly among the ground species, due possibly to populations living on harder or softer ground. In all species odd specimens may also be found occasionally with stubby claws, due to some deformity or accident, and these have not been included in the measurements : similarly occasional specimens may be found with exceptionally long claws in which the tapered tip, which is very fine and delicate, has not worn down as much as usual.

Tail Pattern

The pattern of white in the tail is another aid to identification within the limits imposed by individual variation. In nearly all species the greater part of the outermost pair of rectrices is white, and specific differences are not obvious, I have therefore concentrated entirely on the pattern in the second outermost pair. In all species this pattern will be found to vary individually but always within strict limits, which have been illustrated. While it is never possible on tail pattern alone to say to which species a pipit belongs, it is usually possible to name a number to which it does not belong.

There is some variability in the clearness of the tail pattern, some species having it always pure white, in others it is always dusky white or buff, in others, such as *A. spinoletta*, it varies racially. Too much reliance should not be placed on this colour variation in single specimens since it is frequently difficult to distinguish a pure white pattern that has become dirty through soil-staining, from one that was dusky white originally. Also in old plumage the pure white loses some of its purity, while dusky white tends to bleach.

Wing Formula

The wagtails and pipits have a distinctive wing noteworthy for the length of the inner secondaries which, in fresh plumage, often equal the longest primaries. They are among the group of passerines that have nine primaries, but the outermost primary is so small as to escape notice. For this reason it has become customary in many text books to ignore this feather and to refer to the outermost fully-developed primary as the first. To avoid confusion I have followed this custom.

Variation in the wing formula and in the number of emarginated primaries in the pipits has been cited as a useful aid to specific identification. While recognizing fully this usefulness I do not believe that too much stress should be laid on this character as a guide to relationship, since Savile (1957) has shown that the wing is one of the avian features most readily adapted in the course of evolution to special requirements, and it is therefore as likely to illustrate convergence as relationship. This adaptability is borne out well in the pipits and, at the same time, they illustrate that more pointed wings are the most efficient for long migrations; even within a species slight variation in shape can usually be correlated with the distance that birds of different races migrate. For example the two pipits with the most pointed wings are the Pechora Pipit, *A. gustavi*, and the European race of the Tree Pipit, *A. t. trivialis*; in both these forms the wing tip is composed only of the first three primaries with the fourth at least 4 mm. shorter. They are, respectively, the only Palaearctic migrants to reach as far south as the Moluccas and South Africa. On the other hand the Himalayan race of the Tree Pipit. *A. t. haringtoni*, which does not move further than the north Indian plains, has a blunter wing with the fourth primary less than 3 mm. shorter than the third.

In more than half the other species the first four primaries form the wing tip with the fourth not more than 2 mm. shorter than the third. These species include all the other migrant Palaearctic forms and some of the resident forms of Africa, Asia, the Americas and Australasia. The remaining species are blunt-winged with the first five primaries forming the wing tip. None of these is a true migrant though some forms may move locally.

Emargination is found on the second and third, and sometimes on the fourth and fifth primaries. It is invariably correlated to the length of the feather so that in the pointed wings, in which the fourth primary is short, only the second and third are emarginated, whereas in the blunt wings, in which the first five primaries are nearly equal, the second to fifth are all emarginated.

In describing the wing formula I have used the term "sub-equal" of a group of primaries that are nearly equal in length but in which the relative lengths vary slightly in different individuals.

JUVENILE PLUMAGE

Two distinct types of juvenile plumage are found among the pipits. In many species the juvenile feathers of the upper parts are edged with white, giving a scalloped effect. A few of these feathers are often retained for some months, especially in the wing coverts, so that first winter birds can usually be recognized. In the other species there is no light edging to the feathers and the juveniles are very similar to the adults : in most of these species there is no way of distinguishing between first winter birds and adults.

In Group A a brief description of the juvenile plumage of all species is given as an aid to identification, but, through lack of young birds of many species, it has not been described in Groups B and C.

SUBSPECIFIC VARIATION, DEFINITION AND INDENTIFICATION

There is possibly more controversy on the number of recognizable subspecies in *Anthus* than in any other genus of comparable size. There are several reasons for this but perhaps the greatest is the difficulty of obtaining birds in fresh plumage actually on their breeding grounds. The only certain residents of any area are birds actually breeding, and these, as has already been noted, are highly unsatisfactory for either colour comparison or measurement, because of the wear in the plumage, so that, while varieties may be seen to exist in non-breeding birds, their ranges are hard to define. Outside the breeding season much remains to be learnt of pipit movements : some forms are true migrants, others are subject to small altitudinal local movements, others move locally in association with the rains : there is thus no certainty that any freshly moulted bird is still on its breeding ground.

Another difficulty in the determination of pipit subspecies is that of micro-populations, or ecological variations. Pipits, through their cryptic coloration, are particularly susceptible to variation under different ecological conditions. Thus micropopulations are found in limited areas recognizable from their immediate neighbours but not necessarily from populations living in approximately the same conditions some distance away. Examples of this can be found in the dark populations of *A. novaeseelandiae* found on mountains in central Africa and Asia, and very bleached populations associated with the limestone pans such as the Etosha and Makarikari Pans of southern Africa. On a larger scale all desert populations are, as would be expected, paler than those from wetter areas.

In deciding which of these varieties can be accepted as subspecies one is confronted by the unsatisfactory character of a subspecies as a taxonomic unit. If its definition is to be accepted as "geographically defined aggregates of local populations which differ taxonomically from other such divisions of a species" (Mayr *et al.*, 1953 : 30) one is forced to be illogical with these varieties. Thus the bleached populations of the pans and the dark populations of the mountains have no range that can be geographically defined and cannot therefore be recognized as subspecies. On the other hand, from the topography of the country, the pale desert birds of southern Africa have a range in the west and centre which can be defined and they can therefore be recognized as a subspecies, *A. n. bocage*, though logically their status in respect to the species as a whole is no different from the bleached or dark varieties. However these difficulties and seeming illogicalities are not confined to pipits and are relatively unimportant as long as they are understood.

A third difficulty in determining subspecies is the vexed question of how many to recognize in a cline. Clinal variation is found throughout most of the Palaearctic and Asian species and in deciding which subspecies to recognize I have been influenced largely by the usefulness, or otherwise, of retaining a name. For instance if a population, intermediate in size, contains a high percentage of specimens which, on measurement, can be identified as belonging to it alone, it seems useful to give it a name, for then a proportion of wintering birds will also be identifiable and their movements can be plotted.

This point introduces the question of subspecfic identification of wintering birds. The majority of regional handbooks which define the characters of subspecies do so in such a confident and assured manner that the student is led to believe that all individual birds can be named. This is certainly not true : it is especially misleading in studying the Palaearctic species in which birds from breeding populations as far apart as Russia and Japan may be found together in winter on the north Indian plains alongside the resident forms. Some individuals can, through some diagnostic character of size or pattern, be identified subspecifically with certainty and ascribed to a particular breeding population : these specimens are of great value in plotting migration routes and local movements. However, in my opinion, any attempt to name others individually which have not wholly diagnostic characters results in the building up in collections of alleged subspecies which bear little relation to the breeding populations of the same name. More can be learnt by studying series of wintering birds from a given area and comparing their characters and ranges of measurement with series of breeding birds. In this way it can be deduced, for example, that the majority of Rock Pipits wintering on the east and southern coasts of Britain belong to the Scandinavian race, *A. spinoletta littoralis*, rather than to the British race, *A. s. petrosus*, although few individuals can be named. Similarly it can be shown that the Tawny Pipits, *A. campestris*, that winter in eastern India are drawn from a different breeding population from those wintering in Africa.

This paper is not, however, concerned with detailed definition of the characters and ranges of subspecies except in so far as they affect specific identification, or in cases where I have additions or corrections to make to accepted views. For the Palaearctic species I have used Vaurie (1954 and 1959) as a basis, and for African species the list prepared by White for the *Check-List of Birds of the World*, vol. 9. Both these authors have answered patiently all my questions and I have been fortunate in being able to work with White on the African pipits ; any revisions to his list, as sent to press, have been discussed with him.

Subspecific variation has not been studied in the Australasian and American species.

GROUP A. PALAEARCTIC, ASIAN, AFRICAN AND AUSTRALASIAN SPECIES WHICH PRESENT DIFFICULTY IN IDENTIFICATION

All the species in this group have a wide range and many are highly migratory : they have few distinctive characters common to all plumages and are therefore the most likely to present difficulties in identification. It seems important to understand these difficulties fully rather than to minimize them. For this reason I have tried to illustrate in the discussion and in the plates the amount of variation found in all characters, rather than to illustrate only a typical pattern, claw, wing or tail, which might indicate a distinctiveness not found in all individuals.

The characters are described under each species, or each geographical group within a species, but the measurements have been grouped in eight tables (Tables 2–9, pp. 275–278) for easy comparison. In the sections on identification of each species notes have been made on how it can best be distinguished from all others likely to occur in the same area.

In the widespread Richard's Pipit, *A. novaeseelandiae*, it is convenient to discuss variation and identification under four geographical groups, but no other species has been divided.

1. ***Anthus novaeseelandiae***—Richard's Pipit

Specific characters.—Variable in size. Above, tawny to dark brown, clearly streaked on head and mantle : below, pale buff or white, the breast spotted with well-defined spots, but these are sparse and confined mostly to the upper breast except in Australasia. The hind claw medium or long, comparatively weak and often rather straight. The first three primaries longest and sub-equal with the fourth slightly shorter except, occasionally, in Australasia : the fifth primary about 7–10 mm. shorter than the fourth : the second, third and fourth emarginated and the fifth slightly emarginated in Australasia. The tail pattern white, the pattern on the inner web of the second outermost rectrix usually in the form of a narrow white streak up more than half the shaft, only slightly wider at the tip ; this is sometimes reduced to a short streak against the shaft, near, or at, the tip ; occasionally, in Africa only, reduced to a mere speck at the tip.

The juvenile has scalloped plumage, with rather darker and heavier spotting on the breast than the adult.

AUSTRALASIAN, MELANESIAN AND PHILIPPINE RACES OF RICHARD'S PIPIT

Characters and variation.—There is still some difference of opinion as to whether or not the African and Asiatic races should be considered conspecific with the Australasian races of Richard's Pipit. Australasian races are generally whiter and more streaked below, and have blunter wings. These are very slight differences but might be sufficient to justify recognizing two species were it not that the Australasian races are linked to the Asiatic races through the small white-bellied *albidus* of Flores and Lombok, the slightly buffier *medius* of Timor and the Moluccas, and the lightly streaked *lugubris* of the Philippines. The slightly blunter wing of the Australasian birds seems likely to indicate that they are more sedentary, rather than to have specific significance. Many subspecies have been separated in the Australian area on slight differences of colour and pattern, and in the New Zealand area island races, *aucklandicus*, *steindachneri* and *chathamensis* are recognized from Auckland, Antipodes and Chatham Islands. The New Guinea *exiguus* is a dark montane form.

It has also been suggested that the resident races of southern Asia should be included with the Australasian races in *A. novaeseelandiae*, and the Palaearctic and African races separated as *A. richardi*. The presence of populations in Annam and south China, *sinensis*, which are intermediate between the two groups, shows that this also would be an artificial and arbitrary division which does not seem justified.

Identification. With the exception of the very distinctive and un-pipit-like *A. gutturalis* of New Guinea, *A. novaeseelandiae* is the only pipit resident in the Australasian area. The Pechora Pipit, *A. gustavi*, winters in Indonesia but can be distinguished by its more pointed wing, richer colour above with heavier streaking extending on to the tail coverts, and some white streaks in the mantle. It also has broader white edges to the wing coverts, more streaks on the breast and flanks and the tail pattern dusky rather than white.

Occasional stragglers of other migrant species may be found as far south as New Guinea, but the only ones likely to be confused with the resident birds are those of other races of *A. novaeseelandiae*. In particular a straggler of the Philippine race, *lugubris*, or *malayensis* of south-east Asia, might be confused with *medius* of the Moluccas. It should be noted that *medius* has a shorter and more curved hind claw than either, is whiter below than *malayensis* and has heavier streaking on the breast than *lugubris*. However, *lugubris* and *malayensis* are not normally migratory and are less likely to be found outside their territory than the migrant races of north Asia. All of these are larger and have buffier underparts than any of the resident Australasian or Melanesian forms.

THE NON-MIGRATORY ASIATIC RACES OF RICHARD'S PIPIT

Characters and variation. The non-migratory pipits breeding in India, Burma, Siam and Indo-China southwards to Ceylon, Sumatra and possibly Borneo, are distinguished from the migratory Palaearctic races by smaller size. There is considerable variability in colour among small breeding populations throughout the area: in particular Col. W. W. Phillips has drawn my attention to the relative darkness of birds from the highlands of Ceylon in comparison with those from the coastal districts. These dark birds can, however, be matched with some from highland districts in Malaya, and it is not therefore practical to subdivide this group on any but broad lines. Three intergrading races are all that I can define—*waitei*, from north-west India is generally greyer and less heavily streaked both above and below: *malayensis* from south of lat. 14° S. in both India and south-east Asia is the most rufous and heavily streaked : *rufulus* links the two, ranging north to Upper Burma, Yunnan and Tonkin in the east, and is intermediate in colour, intergrading with both *malayensis* and *waitei*.

There is also indication of a slightly larger breeding population in Annam which is worthy of note only because it may be a step in the cline between the smaller southern and the larger northern races.

In all this group there is haphazard partial moult throughout the non-breeding season.

Identification—subspecific. Table 3 shows how the resident southern races can usually be distinguished on size alone from the migrant races. In India and Burma the only overlap in size is between males of the resident races and females of the migrant races. In Indo-China and Thailand a small proportion of winter visitors of the Chinese race, *sinensis*, cannot be distinguished from the resident *rufulus* or from the Annam population.

Identification—specific. In the east there is no other pipit with which birds of this group are likely to be confused, but in north-west India *A. n. waitei* and the smaller race of the Tawny Pipit, *A. campestris kastschenkoi*, are very similar. They can be distinguished by some minor differences in the relative lengths of the tarsus and wing, and in the structure of the hind claw, bill and wing. These will be discussed more fully under *A. campestris*.

Similarly a small female of the migrant *A. godlewskii* could be confused with large males of both resident races of Richard's Pipit but has slight differences in size and tail pattern which will be discussed under that species.

Among other pipits which may occur in winter in northern India, only some autumn birds of *A. cervinus*, which have not acquired the red throat, are at all similar in colour, pattern and size to the resident Richard's Pipits : these Red-throated Pipits can be distinguished by the streaking on the breast being darker, more clearly defined and extending further down the breast. They are also darker, less tawny, brown with a streaked rump and slight differences in tail pattern and wing formula.

THE MIGRATORY PALAEARCTIC RACES OF RICHARD'S PIPIT

Characters and variation. The large races of Richard's Pipit breed across Asia from western Siberia and migrate chiefly to southern Asia, but stragglers have occurred in many countries from Britain and Lake Chad to Borneo and New Guinea. Breeding birds have been divided into several races on combinations of colour and size, but variation is still imperfectly understood owing to lack of adequate breeding series throughout Siberia and central Asia. A large, rather dark race, *A. n. richardi*, breeds in western Siberia ; a smaller, paler race, *A. n. dauricus*, in Transbaikal ; a large race, *centralasiae*, from Tian Shan eastwards is said also to be pale, though this is not apparent in the few specimens studied ; a small, dark, semi-migratory race, *sinensis*, breeds in South China, and a darker race, *ussuriensis*, in east Siberia and north China is intermediate in size between *sinensis* and *richardi* (*ussuriensis* is considered a synonym of *sinensis* by Vaurie but a fairly extensive series of breeding birds from south China indicates that there is little overlap in measurements between birds of the two populations)

In Table 3 measurements quoted by Vaurie and other workers that are outside the dimensional limits of specimens measured personally, are included in brackets, since my own are obtained from very short series of breeding birds.

It has already been noted in the discussion on moult that all the migrant races of Richard's Pipit are particularly subject to haphazard winter moult. This enhances the difficulties of using colour and pattern in the identification of wintering birds, since no two specimens are ever in truly comparable plumage. Since dimensions are only diagnostic in a very small proportion of birds of the four Siberian races I consider it is best to refer to all wintering birds of these races collectively as *A. n. richardi* subspp.

Identification. Distinction between the Palaearctic and resident races has been shown to be chiefly in size and is illustrated in Table 3.

Specifically *A. n. richardi* subspp. cannot be distinguished in the colour and pattern of the plumage from *A. godlewskii*, but are a richer colour and usually more heavily marked above and below than *A. campestris.* Detailed difference will be discussed under those two species.

The other large pipits of Asia are not likely to be confused with Richard's Pipit. *A. nilghiriensis* of the Nilgiri Hills is not unlike in colour but is short-winged with streaking on the lower breast and flanks. *A. sylvanus* of the Himalayas is also short-winged with very fine streaking below, and *A. similis* is a comparatively unpatterned species both above and below. All have blunter wings and other differences in tail pattern and in the conformation of the hind claw.

Migrants to Europe and Africa of *A. n. richardi* subspp. are also unlikely to be confused with any endemic African or European species but it seems very possible that a straggler to north-east Africa would be overlooked among the resident races of Richard's Pipit, *A. n. cinnamomeus.* Dimensions are the most reliable guide in distinguishing between them, *cinnamomeus* having a usually shorter tail and tarsus, but, in addition, the African birds are usually less heavily patterned above due to the feathers having darker edges contrasting less with the dark centres.

AFRICAN RACES OF RICHARD'S PIPIT

Characters and variation. Richard's Pipit is found through south, east and central Africa westwards to the Cameroons, though it is inexplicably absent from any of the countries of the Middle East except as an occasional migrant. Taxonomically the varying African populations form a most unsatisfactory group though, at the same time, their inconsistencies give rise to fascinating speculation on their relationships and origins. Too little is known of some of the most interesting forms to go far with this at present and it is outside the scope of this paper except in so far as it is necessary to recognize that in central and southern Africa there are three isolated atypical forms, *lwenarum*, *editus* and *hoeschi* which seem more closely linked to each other than to surrounding races. This suggests that there has been a double invasion of the territory and that the atypical birds represent an older population. The two isolated western races, *cameroonensis* and *lynesi*, have also some atypical characters and it is convenient to discuss all these atypical forms separately from the other races.

Typical races of *A. novaeseelandiae* are found in the eastern half of the country from Abyssinia southwards, and in the whole south and south-west. They have the same general colour and pattern as Asiatic forms but with the patterning not quite so distinct on the mantle. They are intermediate in size between the resident and migratory Asiatic races but with a shorter tarsus in relation to the wing: the hind claw never reaches the exaggerated lengths of some Asiatic birds and is commonly about 12 or 13 mm. long: the tail pattern on the second outermost rectrix is commonly the typical elongated streak up the shaft but in occasional specimens of central Africa it is reduced to a little more than a white tip. These specimens will be discussed with the atypical races. There are also examples, notably among darker, montane varieties, in which the pure white in the tail is replaced by dusky white.

The protracted breeding season of African pipits makes it difficult to study the sequence of moult, but it is apparent that in most populations there are two peak periods in the year, probably corresponding to the normal complete post-breeding moult and the partial pre-nuptial moult. However, the preponderance of specimens collected in other months in which there are feathers in sheath, or some recently moulted feathers, suggests that African as well as Asiatic birds are subject to haphazard off-season moult.

White (1957) has shown that it is impractical to recognize more than three races among the typical populations. These correspond to the three resident races of Asia. The tropical *cinnamomeus* is the most heavily streaked and corresponds to *malayensis*: the sub-tropical *bocagei* of the dry south-west is the palest, greyest, and least heavily streaked and corresponds to *waitei* of the Punjab: *rufuloides* of the wetter south-east, north about to the Zambezi, is intermediate and corresponds to *rufulus*. As in Asia there are recognizable micro-populations in different ecological conditions: very dark birds are associated with the mountains of the eastern Congo, Tanganyika and Nyasaland; rather more richly coloured birds with areas of red soil (though in many cases the rich appearance is largely due to soil-staining): within the paler race there are exceptionally bleached populations associated with limestone pans such as the Etosha and Makarikari Pans. Though names have been given to many of these varieties their discontinuous distribution precludes them being recognized as true subspecies.

The three southern atypical forms, *lwenarum*, *editus* and *hoeschi*, which I have suggested belong to an older population, have also a discontinuous distribution within the range of the typical forms. All three are large and rather dark, unique in having the pattern of the second outermost rectrix reduced to a tiny spot: the pattern on the outermost is dusky rather than pure white. The race *lwenarum* from north-western Rhodesia is also uncharacteristic of *A. novaeseelandiae* in having the dark centres of the mantle feathers and the spots on the breast ill-defined, giving a less streaky effect. The Basutoland *editus* has exceptionally dark centres to the mantle feathers. The South West African *hoeschi* is known only from two specimens, of which the type only has been examined. It is similar in size and in colour above to *lwenarum*, below the spotting on the breast is closer to *bocagei*: the tail pattern is reduced to a spot on one second outermost rectrix and a tiny faint streak on the other.

It has already been noted that the abnormal reduction in the tail pattern is found occasionally in specimens of *cinnamomeus* near the range of *lwenarum*, and so is the dusky white of the tail pattern.

The two atypical western races, *cameroonensis* and *lynesi*, are both dark with heavy streaking on the breast : *cameroonensis* of Mt. Cameroon is paler below and rather greyer above than *lynesi*, which has rich buff underparts. Apparently *lynesi* occupies other montane areas in the Cameroons, migrating as far as Darfur in May and June. These two races differ from others in having consistently shorter hind claws, never over 11 mm., and in having the tail pattern dusky (*cameroonensis*) or buff (*lynesi*), but of the typical elongated pattern.

Identification. In general colour and pattern the African forms of *A. novaeseelandiae* and *A. similis* are very alike, *similis* being only slightly less distinctly streaked. Chapin (1937) has pointed out that they can be distinguished by the fifth primary, which is emarginated in *similis* but not in *novaeseelandiae*. This is not, however, always easy to determine in worn or damaged specimens and a further check is provided by the relative lengths of the inner primaries, particularly the difference between the fourth and fifth which in *novaeseelandiae* is about 7–9 mm. so that the wing tip appears to be formed of the first four primaries ; in *similis* the difference is less than 4 mm. so that the first five form the wing tip. The majority of specimens of *A. novaeseelandiae* can also be distinguished by the elongated tail pattern and the long hind claw, but the wing is an additional ând surer check where atypical forms of *novaeseelandiae* occur, especially in central Africa, for here *A. similis* has also an atypical form, *A. s. schoutedeni*, with a tail pattern similar to that of *A. novaeseelandiae.*

Very worn specimens of Richard's Pipit, which have lost the pattern on the mantle, might also be confused with the plain backed species, *A. leucophrys* and *A. vaalensis*, which have the same wing formula. In all but atypical *A. novaeseelandiae* the whiteness and extent of the tail pattern should be diagnostic, and in most cases the measurements as well, since *A. novaeseelandiae* is usually smaller with a shorter tail than sympatric Plain-backed Pipits.

The migrant, *A. trivialis*, has a shorter bill, more extensive streaking on the breast, a different wing formula and hind claw.

2. ***Anthus godlewskii***—Blyth's Pipit

Specific characters. Large. Above, tawny brown, clearly streaked or head and mantle : below, pale buff, the breast spotted with well-defined spots, but these are sparse and confined mostly to the upper breast. The hind claw of medium length and comparatively weak. The first three primaries longest and sub-equal with the fourth slightly shorter : the fifth about 10 mm. shorter than the fourth : the second, third and fourth emarginated. The tail pattern white with the pattern on the second outermost rectrix a triangle, broad at the tip and tapering to a point close to the shaft not more than 30 mm from the tip and usually about 15 mm. : occasionally reduced further but always retaining a triangular shape rather than appearing as a streak along the shaft.

Blyth's Pipit has a haphazard winter moult and a partial spring moult, similar to Richard's Pipit, in the body feathers, innermost secondaries, wing coverts and central rectrices, but no specimens have been examined in which primaries or other rectrices have been in winter moult.

The juvenile has scalloped plumage and below the spotting is slightly denser and darker but less well-defined than in the adult.

Range. Breeds in central Asia from Transbaikal and eastern Manchuria to Tibet and Assam, migrating to India, Ceylon, Andaman Islands, Burma and Yunnan. It has once been found at Lake Chad (White, 1957 : 33).

Geographical variation. None recognized.

Identification. The identification of Blyth's Pipit was discussed fully (Hall, 1957) : it was found that individual specimens are quite indistinguishable in colour and pattern from *A. novaeseelandiae richardi* subspp., except for the tail pattern. The triangular shape, as distinct from the elongated shaft streak, is diagnostic in the majority of specimens but in the extreme variations when the triangle is most elongated or greatly reduced it is not so easy to recognize.

In series it is just apparent that the spots on the breast of Blyth's Pipit are rather more sharply defined and triangular.

A. godlewskii can, however, be best distinguished from all Asiatic races of Richard's Pipit by the relative length of wing and tarsus, though the difference is fine. In the length of the wing and tail *A. godlewskii* is similar to the migratory races, *A. novaeseelandiae richardi* subspp., but has a tarsus 24–28 mm. against 28–33 mm. It has a longer wing and tail than the resident races but a similar tarsus. There is a small overlap in overall dimensions with *A. n. sinensis* which can be resolved by taking the wing/tarsus ratio into account as this in *A. godlewskii* is 3·2–3·8, against 2·9–3·1 in *sinensis*.

Added to the differences in dimensions and tail patterns it will be found that the length of the hind claw in many migrant specimens of Richard's Pipit is wholly diagnostic, since in *A. godlewskii* it is rarely over 14 mm.* and in the rare extreme cases the weak tapering tip is curved sharply, while in *A. n. richardi* subspp. the claw is rarely under 15 mm. with a straighter tip. In series the legs of *A. godlewskii* in the dried skin appear paler than those of *A. novaeseelandiae*.

There are therefore several fine distinctions on which these two species can be distinguished but it is advisable to take all into consideration.

A. godlewskii is generally more heavily streaked above and below than *A. campestris*, but confusion might arise in comparing worn skins with young *campestris* which are more heavily streaked than the adults. Table 5 shows that *A. godlewskii* has usually a shorter bill than *A. c. campestris* and a longer wing than the eastern race *A. c. kastschenkoi*. In addition *A. campestris* has a similar elongated tail pattern to *A. novaeseelandiae*, and a slightly stouter, more curved hind claw.

3. ***Anthus campestris***—Tawny Pipit

Specific characters. Large. Above, light or tawny brown, indistinctly streaked on the head and mantle in adults : below, pale buff, with little or no spotting on the breast in adults : the young bird quite distinctly streaked above and on the breast. The hind claw short to medium, curved and moderately strong. The first three primaries longest and sub-equal with the fourth slightly shorter : the fifth about 10 mm. shorter than the fourth : the second, third and fourth emarginated. The tail pattern white with the pattern on the second outermost rectrix usually in the form of a long narrow streak up the shaft, only slightly wider at the tip : this is sometimes reduced to a short streak near the tip.

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* Hall (1957 : 730) recorded in error the maximum length as 17 mm. This should be 15 mm.

The Tawny Pipit has a haphazard winter moult of some body feathers, wing coverts, innermost secondaries and central rectrices, and a partial spring moult into similar plumage.

The juvenile has scalloped plumage and distinct dark spotting on the upper breast.

Range. Breeds in the Palaearctic region westwards from the Yenisei to Britain (one record) and south to northern India, Palestine and the Atlas Mts. Winters also in southern India, Arabia and Africa north of the equator.

Geographical variation. There is considerable local variation in colour from sandy to greyish among the Tawny Pipits, with a higher proportion of greyer birds in the east, and some conspicuously pale birds breeding in parts of the Middle East, but these variations seem to be ecological and discontinuous rather than geographical and no races are here recognized on colour alone. There is, however, a significant decrease in size eastwards and I recognize *A. c. kastschenkoi* as a smaller race breeding between the Ob and Yenisei rivers, and wintering in India. Measurements of all Indian wintering birds show that both *A. c. campestris* and *A. c. kastschenkoi* winter in the west of the country, and many specimens are indeterminate, but that *kastschenkoi* alone winters in the east, in United Provinces and Bihar. In series *kastschenkoi* is rather greyer than *campestris.* The smaller, greyer Indian birds were formerly known as *A. c. griseus,* described from Tian Shan, but it has since been found (Hall, 1957) that Tian Shan birds are not smaller than European birds, so that *griseus* is considered a synonym of *campestris.*

Identification. The plainer back and plain breast of the majority of the specimens of the Tawny Pipit serve to distinguish it from all other pipits in the area except for some races of *A. similis* : these, however, can always be recognized by their blunter wings, dusky and reduced tail pattern and usually by longer tails.

First winter birds and some adults of *A. campestris* which have retained some spotting on the breast are not, however, easily distinguishable from some Richard's Pipits, which have a similar wing formula and tail pattern. In particular some specimens of the small *A. c. kastschenkoi* are easily confused with the paler, lightly streaked *A. n. waitei* in north-west India. The best guides to identification are the relatively short tarsus and long wing of *A. campestris* and its shorter and more curved hind claw and finer bill. In the dried skin the bill and legs of *A. campestris* are usually paler than those of *A. novaeseelandiae.*

The same principles of identification apply to juveniles as to adults but the fact that measurements are useless makes it difficult to identify all juveniles of *A. campestris, A. novaeseelandiae* and *A. godlewskii* with certainty.

4. *Anthus similis*—Long-billed or Indian Rock Pipit

Specific characters. Large with a long tail, except in central and west Africa. Above, variable in colour from light to dark brown, with the streaking on the head and mantle sometimes very indistinct, sometimes heavy, but never sharply defined except in first winter birds: below, light to rich buff, with the streaking on the breast variable, sometimes very indistinct and sparse, sometimes dark and extending to the lower breast, but never very sharply defined. The hind claw short, curved and strong. The first four primaries longest and sub-equal with the fifth never more than 8 mm. shorter than the fourth and usually under 5 mm. shorter, so that the first five primaries from the wing tip: the second to fifth primaries emarginated. The tail pattern dusky white or buff and the pattern on the inner web of the second outermost rectrix limited to a small triangle near the tip except in one atypical form in central Africa, *schoutedeni.*

A. similis has no apparent winter or spring moult, and the plumage does not seem to wear as quickly as that of other species that have been discussed.

The juvenile has scalloped plumage and has well-defined spotting, rather than streaking, on the breast.

Range. Breeds in suitable territory in most of Africa south of the Sahara, Sokotra, Arabia, and from Palestine to India with an isolated population in central Burma. Not truly migratory but subject to local movement, particularly in the sub-tropical forms which come down from the hills in winter.

Geographical variation. About twenty races are recognized varying for the most part in small degrees of colour, patterning and size. There are broadly two groups, one of the almost unstreaked races found in the sub-tropics and the other of the more heavily patterned tropical races.

The plain-backed Asiatic races include the large, sandy *jerdoni* of north-eastern India, the greyer *decaptus* of north-western India westwards to Iraq, and the small grey *captus* of Palestine. The large dark races, *travancoriensis* and *similis* of southern India, and the smaller *yamethini* of central Burma, are more heavily patterned: in *travancoriensis* the triangular pattern on the second outermost rectrix is consistently of the more extensive varieties (illustrated as 1 and 2 on Plate 60) which are found only rarely in other Asiatic forms. Both *arabicus* and the long billed *sokotrae* are small and heavily patterned. In Africa north of the equator *nivescens, jebelmarrae* and *asbenaicus* are less heavily patterned than the races of eastern and central Africa, *hararensis, hallae, nyassae, dewittei* and *schoutedeni*, and the dark *bannermani* and *josensis* of West Africa. South of the Zambezi the races *leucocraspedon* and *nicholsoni* are again less heavily patterned.

None of these races show any noteworthy characters except for *jebelmarrae* and *asbenaicus* of Darfur and the Sahara, and *schoutedeni* of the southern Congo and Angola. In *jebelmarrae* and *asbenaicus* the tail pattern is heavily reduced, so that it is absent or a mere tip, on the second outermost rectrix and confined to a small triangular pattern on the outermost: in *schoutedeni* the tail pattern on the second outermost rectrix is often elongated in a streak up the shaft and nearly as extensive as in *novaeseelandiae*. Furthermore *schoutedeni* shows other approaches to *novaese-*

elandiae in having the patterning above and below more clearly defined than is usual in *similis* and the breast spotted rather than streaked ; the bill is also shorter than is common in *similis*. The range of *schoutedeni* is from the middle Congo river through the Kasai to Angola and north-western Rhodesia, but occasional specimens of the more eastern *nyassae* have either the short bill or the elongated tail-pattern of *schoutedeni*.

Identification.—In Asia the plainer races of *A. similis* bear a superficial resemblance to *A. campestris*, and the more heavily patterned races to migrants of *A. novaeseelandiae* and *A. godlewskii*. They can all be distinguished by the blunter wings and different tail pattern, and usually also by the length of the tail and hind claw.

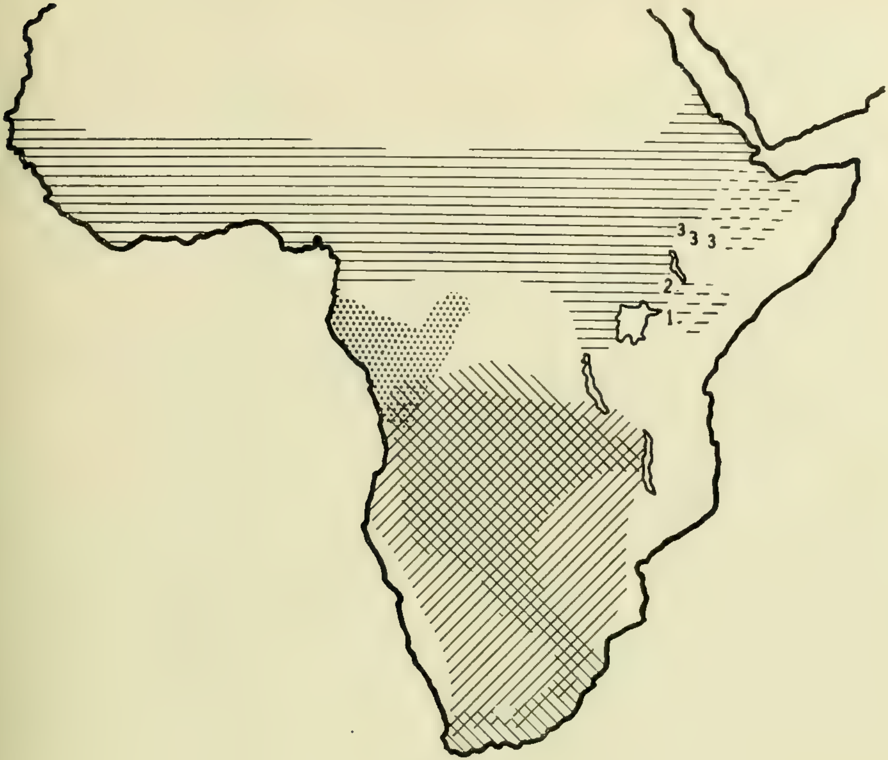
In Africa as in Asia there is the same superficial resemblance between many of the races of *A. similis* and *A. novaeseelandiae* and through most of the country the same specific differences of wing formula and tail pattern are diagnostic, in addition to the more sharply patterned appearance of *A. novaeseelandiae*, the straighter hind claw and usually shorter tail. It cannot, however, be emphasized too strongly that in parts of central Africa, within or bordering the ranges of *A. novaeseelandiae lwenarum* and *A. similis schoutedeni*, all these distinctions are not diagnostic, for these two races both show an approach in some characters to the other species. Thus *lwenarum* has the dusky restricted tail pattern and ill-defined streaking above typical elsewhere of *A. similis*, and *schoutedeni* has the extensive tail pattern, more sharply defined pattern above and shorter bill typical elsewhere of *A. novaeseelandiae*. In this area therefore the surest guide to identification is the blunter wing and longer emarginated fifth primary of *A. similis*, with the shape of the hind claw as an additional check.

Even the least patterned races of *A. similis* in fresh plumage are distinguished by the amount of streaking on the mantle from the Plain-backed Pipits, *A. vaalensis*, *A. leucophrys* and *A. pallidiventris*, but very worn birds present greater difficulty. The wing formula is some help, but not a certain guide since the fifth primary of some of the Plain-backed Pipits has some emargination and is frequently only 5 mm. shorter than the fourth, though the difference is never less than that. The tail pattern may also be diagnostic since the typical *similis* triangle is found only rarely in Plain-backed Pipits in southern Africa, in some specimens of *A. vaalensis*, or, in northern Africa, as a very dusky and ill-defined pattern in some specimens of *A. leucophrys*. Dimensions may be a guide as well, particularly the usually longer bill and tail of *A. similis*, and many Plain-backed Pipits have a longer, straighter and weaker hind claw.

5. ***Anthus vaalensis, A. leucophrys*** and ***A. pallidiventris***—the Plain-backed Pipits

The Superspecies.—The relationship of the three plain backed species of African pipit is so complex and still so little understood that it is convenient to consider them as a superspecies and discuss them together. From the data at present available it seems that in South Africa there are two sibling species, *A. vaalensis* and *A. leucophrys*, which show some different ecological preferences and which can be dis-

Map to Show Distribution of Plain-backed Pipits



Key

░ *A. pallidiventris.*

Southern Africa.

▧ *A. leucophrys*
(*leucophrys, bohndorffi*).

▨ *A. vaalensis*
(*vaalensis, chobiensis, neumanni*).

Northern Africa. (*A. leucophrys*).

▤ Dark races
(*omoensis, zenkeri, ansorgei, gouldii*)

┅ Light races
(*saphiroi, goodsoni*).

1. Area where *zenkeri* and *goodsoni* have been found together.

2. Intergrade between *zenkeri* and *goodsoni.*

3. Intergrades between *zenkeri* and *saphiroi.*

tinguished in the hand by colour, size and the relative lengths of the hind claw : there is also some slight difference in tail pattern. Northwards, in Angola, Northern Rhodesia and Nyasaland, the differences are less well marked but just apparent. Northwards again there is a strip across Africa through the Belgian Congo and Tanganyika from which *A. vaalensis* and *A. leucophrys* are absent but in the west of which the long legged *A. pallidiventris* is found. From West Africa to Kenya, north of this strip, there is no reliable evidence of two species being present, light and dark populations of the *leucophrys/vaalensis* types being alopatric and linked by intergrades : there is no corelation between lightness of colour, size and the length of the hind claw, as in South Africa, and furthermore both types of tail pattern associated with the different species in South Africa are found haphazard in the north among individuals of varying colours. White (1948) hitherto has believed both *A. vaalensis* and *A. leucophrys* to be present in the north, basing his conclusion on the record of both light and dark birds being found together near Lake Naivasha in Kenya. However, since this is the only area of overlap and lies between the ranges of darker and paler populations it does not necessarily imply that the two forms breed alongside : it is quite possible that some of these were non-breeding birds from neighbouring areas, and if this is so only one species need be recognized in the north.

I suggest tentatively that, in the course of evolution, the Congo population was at some time isolated and developed as a good species, *A. pallidiventris* ; elsewhere two other species, *A. vaalensis* and *A. leucophrys*, developed through some ecological preferences, but, before speciation was complete, some change in climate or vegetation in the north broke down the ecological barrier and the two re-united there, forming a single semi-hybrid, species. Taxonomy cannot give a picture of these relationships and I therefore propose for convenience to treat *A. pallidiventris* as a distinct species and to recognize both *A. vaalensis* and *A. leucophrys* in southern Africa, but refer all northern forms to *A. leucophrys*.

Characters of the Superspecies.—Large. Above, tawny to dark brown, with slight obsolescent streaks on the head : below, light buff, with light, ill-defined streaking confined to the upper breast. Hind claw variable, from fairly long and strong (*pallidiventris*, and *leucophrys* in S. Africa) to short and weak (*vaalensis* in S. Africa) The first four primaries longest and sub-equal with the fifth 5 10 mm. shorter than the fourth : the second to fourth emarginated, and the fifth sometimes slightly so. The tail pattern dusky or buff with the pattern on the second outermost rectrix frequently reduced to a mere spot, occasionally a well-defined triangle near the tip (some specimens of *vaalensis* in South Africa), occasionally an elongated streak along the shaft (*leucophrys* in South Africa), all variations being found in northern Africa.

The Plain-backed Pipits do not appear to have any off-season or pre-nuptial moult.

The juveniles have scalloped plumage with distinct streaking on the breast.

Ranges (see Map.)—In southern Africa *A. leucophrys* ranges from Cape Province, Natal, Transvaal through northern Bechuanaland and northern South West Africa to Angola, Northern Rhodesia, southern Belgian Congo and Nyasaland. *A. vaalensis* ranges from Cape Province north through South West Africa, Bechuanaland and the Transvaal to Angola, southern Belgian Congo, Nyasaland and Portuguese East Africa. *A. pallidiventris* is found in Spanish Guinea, Gaboon, the Lower

Congo, and extreme northern Angola. In northern Africa *A. leucophrys* ranges from Portuguese Guinea to British Somaliland south to the northern Belgian Congo and Kenya.

Geographical variation.—In South Africa *A.v. vaalensis* is large, sandy-coloured with a short, weak hind claw, and sometimes with a small well-defined triangular spot on the second outermost rectrix : it is replaced northwards from Angola to Nyasaland by *A.v. neumanni* which is a smaller and less sandy race, variable in colour with lighter and darker populations interspersed (Hall, 1959) : in *neumanni* the tail pattern is invariably a mere spot. Birds from Southern Rhodesia are intermediate. *A.l. leucophrys* in southern Africa is a smaller, darker bird than *A. v. vaalensis* with a longer, straighter and stronger hind claw : it has commonly an elongated streak up the shaft on the second outermost rectrix, and has also been found sometimes to have a bright yellow lower mandible, in contrast to the invariably duller bill of *A. vaalensis*. The variation in bill colour in *A. leucophrys* is not fully understood but is probably seasonal. In central Angola and Northern Rhodesia *A.l. leucophrys* is replaced by the darker *A.l. bohndorffi*, which, like *A.v. neumanni*, has little or no pattern on the second outermost rectrix. A single rather grey specimen of *A. leucophrys* has been examined from Duque de Bragança in northern Angola, and four very dark specimens were examined by White from Thysville, Lower Congo, none of which can at present be referred to any race.

A. pallidiventris differs from *A. leucophrys* in its stronger, and usually longer, leg, stronger foot with longer hind toe, and stronger hind claw. The tarsus measurements show a slight overlap at 30 mm. but the relatively greater strength of the leg of *pallidiventris* is always apparent. In addition there is some difference in the bill structure, the nostrils of *pallidiventris* being more exposed, giving the bill the appearance of being longer, although the measurements from the base of the skull may be the same as in *leucophrys*. *A.p. pallidiventris* in Gaboon and the Lower Congo is darker than *A.p. esobe* which is found further up the river near Coquilhatville : a single specimen examined from Luanda, northern Angola, matches closely with *esobe*.

The forms of northern Africa ascribed to *leucophrys* vary from the dark and small *gouldi* and *ansorgei* in West Africa, and the dark *omoensis* of northern Abyssinia, to the light brown *saphiroi* of southern Abyssinia and the even lighter *goodsoni* of Kenya. Most of the range from northern Nigeria to the borders of Kenya and south-west Abyssinia is occupied by *zenkeri* which is a comparatively dark bird, varying in different populations but browner than the other dark races. Intermediates between *zenkeri* and *saphiroi* are found in south-west Abyssinia (Uba, Konso and Mega), and one intermediate between *zenkeri* and *goodsoni* has been examined from Eldoret in north-west Kenya : both *goodsoni* and *zenkeri* have been found between Nakuru and the Mara River, as has already been noted.

In the paler races, *goodsoni* and *saphiroi*, there is some consistency in the hind claw, which is never very long, and in the tail pattern which is never elongated : in these respects these races show the characters of *vaalensis*. In the darker races however, every variation of tail pattern is found, sometimes well-defined and sometimes so dark as to be almost indistinguishable, and the hind claw varies from 9–18 mm. It is this degree of variation in two characters which are so often specifically diagnostic that makes me suggest that this is a hybrid population.

Identification.—Distinctions between the Plain-backed Pipits and worn specimens of *A. similis* have been discussed under that species. Worn specimens of *A. novaeseelandiae* are unlikely to lose all trace of patterning but can also usually be recognized by the white and clearly defined tail pattern.

Distinctions between the three species of Plain-backed Pipit have been discussed under geographical variation but can be summarized briefly as follows :—

South Africa.—*A.v. vaalensis* larger, paler and with shorter hind claw than *A.l. leucophrys*, with occasional differences in tail pattern.

Southern central Africa.—*A. vaalensis neumanni* less easily distinguished from *A.l. leucophrys* and *A.l. bohndorffi* owing to similarity in size, and variability in colour, but paler in all variations than the latter, and with the hind claw weaker and usually shorter. The lower mandible of *A. leucophrys* sometimes bright yellow.

West central Africa.—*A. pallidiventris* with a stronger and usually longer leg than *A. leucophrys* and a more exposed bill.

6. *Anthus pratensis*—Meadow Pipit

Specific characters.—Medium sized. Above, olive brown, with clear streaking on head and mantle : below, white or light buff, with spotting on the breast dark and well-defined, changing on the lower breast and flanks to sparse streaks. The hind claw fairly long and weak. The first three primaries longest and equal, the fourth usually less than 1 mm. shorter, occasionally 2 mm.: the second, third and fourth emarginated. The tail pattern white with a small triangle, spot or streak near the tip of the second outermost rectrix, never very extensive : the primaries and rectrices sometimes rather pointed.

The Meadow Pipit has a partial moult into similar plumage between January and March. This is usually limited to the body, central rectrices, innnermost secondaries and some wing coverts.

The juvenile is not scalloped and resembles the adult except that the streaking is more extensive on the underparts and heavier above and below : the mantle is a richer, redder brown, less olive than the adult, but the edges of the wings are olive brown as in the adult.

Range.—Breeds from south-east Greenland to western Siberia, south to southern France, northern Italy and the Balkans : winters in Europe, north Africa, the Middle East and Turkestan.

Geographical Variation.—There is a cline in colour from the richest birds in the west to the greyest in the east of the range. The name *theresae* was given to the richest coloured birds, based on some collected in Ireland in autumn, and believed by Williamson (1959) to belong to the breeding population of Iceland. It is possible to identify as *theresae* a few exceptionally richly coloured specimens among winter birds from other parts of Britain and western Europe and also to recognize in series that the rest of the wintering birds of Britain are richer coloured than those of Europe and North Africa. It may be assumed therefore that they are drawn from a breeding population intermediate between *theresae* and *pratensis*, probably from Scotland and the Hebrides. Ringing has shown that birds breeding in England move south to winter.

Identification.—The combination of small size, short bill and olive brown edges to the wings distinguish the Meadow Pipit from all the species that have been discussed previously. It is most likely to be confused with the Tree Pipit, *A. trivialis*, but has a finer bill and a longer and less curved hind claw : the markings on the breast of *A. pratensis* are also usually rather less heavy and, in Europe, the difference between the third and fourth primaries of *A. trivialis* is usually greater than 2 mm.

The Pechora Pipit, *A. gustavi*, and some female and young Red-throated Pipits, *A. cervinus*, are similar in size and not unlike in colour to the Meadow Pipit, but have lighter edges to the feathers of the mantle and head, streaked upper tail coverts, whiter edges to the wing coverts, and plain brown, not olive brown, edges to the wings. *A. gustavi* has, in addition, a distinctive tail pattern and wing formula.

7. ***Anthus trivialis***—Tree Pipit

Specific characters.—Medium sized. Above, light brown to olive brown, with clear streaking on head and mantle : below, white or light buff, with spotting on the upper breast dark and well-defined, changing on the lower breast to sparse, narrow streaks. The hind claw short and curved. The first three primaries longest and equal, the fourth commonly about 5 mm. shorter than the third in western birds, and 1–2 mm. shorter in Indian birds : the second and third emarginated, the fourth slightly emarginated in western birds and more clearly in Indian birds. The tail pattern slightly off white with the pattern on the second outermost rectrix a small spot, triangle or streak near the tip of the inner web, never very extensive : the rectrices usually rather pointed.

The Tree Pipit has a partial moult of body feathers, taking place in January and coming into similar plumage.

The juvenile is not scalloped and resembles the adult except that the streaking is heavier below and the general colour above is slightly redder brown.

Range.—Breeds in most of Europe and western Asia to Lake Baikal, between latitudes 40° N. and 70° N.: winters throughout Africa, south to the Transvaal, in the Mediterranean region, Persia and most of India.

Geographical variation.—Siberian breeding birds tend to be greyer than European, especially on the upper tail coverts, and have been separated as *sibirica* : they also have frequently more white in the tail, the more elongated pattern being common : the fourth primary is usually 2–3 mm. shorter than the third, against 4–5 mm. in western birds of typical *trivialis*. None of these characters is constant and I do not believe it is practical to attempt to differentiate between wintering birds of *trivialis* and *sibirica* though the names may be retained for the breeding populations.

There is also some clinal variation in size, the largest birds breeding in Russia, where the wings of males may reach 95 mm. and Scandinavia (♂ 87–90) : breeding birds from Britain and France are smaller (♂ 84–87) and so is *sibirica* (♂ 81–88). No wintering birds with wings over 90 mm. have been examined from West Africa or

India and it can therefore be assumed that the Russian population winters exclusively in eastern Africa.

In Turkestan and the north-western Himalayas there is a very distinct race, *haringtoni*, in which the markings on the head, mantle and breast are darker and heavier, the bill is stouter and the difference between the third and fourth primaries is less than 3 mm. No breeding birds examined show intergradation between *haringtoni* and *trivialis* or *sibirica* but some wintering birds of northern India show one or other of the characters, and may be presumed to belong to some intermediate population. In winter *haringtoni* moves down to the plains of northern India but does not undertake the vast migrations of *trivialis* and *sibirica*.

Identification.—The Tree Pipit is most likely, in Europe, to be confused with the Meadow Pipit, *A. pratensis*, but has a stouter bill and a distinctive short, curved, hind claw. The markings on the breast are usually more extensive and, in Europe, the fourth primary is usually shorter.

Among other characters the stout bill and unstreaked upper tail coverts distinguish the Tree Pipit from the young Red-throated Pipit, *A. cervinus*, and the Pechora Pipit, *A. gustavi*. The lack of green tone in the plumage or green edges to the wings distinguish it from the Indian Tree Pipit, *A. hodgsoni*.

In central and southern Africa the wintering Tree Pipit is best distinguished by its short bill, legs and hind claw from the resident races of *A. novaeseelandiae*, and by its short legs, clear streaking and pointed wing from those of *A. similis*.

8. ***Anthus hodgsoni***—Indian Tree Pipit

Specific characters.—Medium sized. Above, olive green with green edges to wing and tail and with blackish streaking on head and mantle varying from very light to heavy : below, white, with dark, broad, well-defined streaking variable in extent. The hind claw short and curved, The first three primaries longest and sub-equal, the fourth 1 4 mm. shorter : the second, third and fourth primaries emarginated. The tail pattern slightly off-white with the pattern on the second outermost rectrix in the form of a small spot or triangle near the tip, sometimes extending about 25 mm. up the shaft.

The Indian Tree Pipit has a partial moult of body plumage and some wing coverts from February to April.

The juvenile is like the adult but more heavily streaked on the mantle and underparts, the streaks wider as well as more extensive : the greens of the plumage are more bronzy, especially on the edges of the wings and wing coverts.

Range.—Breeds from the Pechora in north-eastern Russia, eastwards to the Kurile Islands and Japan, southwards to the Himalayas and Szechwan. Winters in India, Burma, Siam, Indo-China, Japan and the Philippine Islands.

Geographical variation.—The most northern breeding birds are the least heavily streaked, both above and below, the streaks in the mantle in fresh plumage being narrow, faint and ill-defined and the streaks below heavily concentrated on the upper breast, extending only sparsely on to the lower breast and flanks. Ripley (1948) has shown that these birds should be called *yunnanensis*. Southern birds, *A. h.*

hodgsoni, breeding from the Himalayas to central China, are more heavily streaked, the streaks on the mantle being black and well-defined, narrow on the mantle and rather broader on the head : the concentrated streaking on the breast extends to the lower breast and there is more streaking on the abdomen. In *yunnanensis* the fourth primary is usually 1–3 mm. shorter than the third, in *hodgsoni* the difference is usually less than 1 mm. These two races therefore show similar differences in pattern and wing formula to those that distinguish the northern and southern populations of *A. trivialis*.

There is, in addition, a population breeding in Japan which is difficult to place taxonomically since it hardly shows sufficiently distinct characters to warrant a name, and yet is not truly typical of either race. It is slightly less heavily streaked than *hodgsoni*, though closer in this character to *hodgsoni* than to *yunnanensis* : it has on average a longer bill and shorter tail than either of the other races (Table 8) : the wing is usually similar to *yunnanensis* and more pointed than *hodgsoni*. These characters are trivial and do not readily identify individual specimens, but they serve to show that most of the wintering birds of Formosa and the Philippines, as well as some of those from Japan and Indo-China, belong to the Japanese breeding population. These birds have sometimes been described as intermediates between *hodsoni* and *yunnanensis* but are not truly intermediate in either the morphological or geographical sense, and it seems preferable to refer to them as an atypical population of *hodgsoni*. Specimens listed as this population in Table 8 include four summer birds from Japan and winter birds from Japan, Formosa and the Philippines which which are distinct from *yunnanensis* on size and/or colour.

Ripley (op. cit.) believed also that there was a distinct population, *A. h. berezowskii*, of very heavily streaked, long billed birds breeding in south-east Tibet and Sikang province, China. This view was based on twelve specimens : two of these he has told me (in litt.) he has since found to be immature *A. roseatus* : through his kindness it has been possible to re-assemble most of the remainder of the series : these have been compared with the exceptionally good series in the British Museum and it was found that all showing very wide streaks were young birds of either *hodgsoni* or *roseatus*, and those with a long bill either *roseatus* or Japanese *hodgsoni*. There are therefore no apparent grounds for recognizing *A. h. berezowskii* as distinct from *A. h. hodgsoni*.

Identification.—The green edges to the wings and the green in the upperparts distinguish *hodgsoni* from all other species except *A. roseatus*. In autumn plumage *A. roseatus* is superficially very similar to the adult *hodgsoni* and even more so to the young bird. The two species can best be distinguished by the hind claw, which is short and curved in *hodgsoni* and longer and weaker in *roseatus* : in addition *roseatus* has a distinctive tuft of lemon yellow in the axillaries, is usually a larger bird with a longer bill, darker legs, and less clear white underparts.

9. *Anthus roseatus**—Hodgson's Pipit

Specific characters.—Medium to large sized. Above, upperparts in autumn olive brown, with dark, wide streaks on head and mantle, edges of wings green : in spring and summer the upperparts are grey and heavily streaked : below, in autumn, white with a faint wash of pink or buff, the breast heavily streaked with the streaking extending to the lower breast and flanks : in spring and summer there is little or no streaking and the chin to the lower breast is a vinous pink : axillaries lemon yellow. The hind claw medium, weak and comparatively straight. The first four primaries longest and sub-equal : the second, third and fourth emarginated. The tail pattern slightly off white, the pattern on the second outermost rectrix confined to a medium or small triangle near the tip.

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* This species may in future have to be known as *A. pelopus* Gray (see Deignan 1960, Bull. Br. Orn. Cl. 80 : 120.)

Hodgson's Pipit has a complete moult of body plumage between December and March into the distinctive breeding dress.

The juvenile plumage is generally similar to that of the adult in autumn but is browner above and less heavily streaked below, with no streaking on the abdomen.

Range.—Breeds in the mountains of central Asia from Afghanistan to China and Tonkin, descending to the plains in winter.

Geographical variation.—None apparent.

Identification.—The green edges to the wing distinguish *A. roseatus* from all other Asiatic species except *A. hodgsoni*. As has already been noted, autumn birds and young birds of the two species can be confused but are distinguishable on the shape of the hind claw, colour of the legs, the lemon yellow axillaries of *A. roseatus*, and sometimes also on size. The spring plumage of *A. roseatus* is quite distinctive since no other pipits have pink on the underparts except the Water Pipit, *A. spinoletta*, in which the pink is less vinous in tone, and the Red-throated Pipit, *A. cervinus*, in which the pink is confined to the throat and upper breast. Furthermore neither of these species have any green in the wings or yellow axillaries.

10. ***Anthus cervinus***—Red-throated Pipit

Specific characters.—Medium sized. Above, tawny brown in autumn, grey brown in spring, distinctly streaked on head, mantle, rump and tail coverts, with some indistinct white streaks on the mantle : wing coverts broadly edged with white : below, pale creamy buff, in autumn clearly streaked with black on the breast, lower breast and flanks, the throat either white or with some orange pink, the pink found more commonly and more extensively in males : in spring males have the throat and breast orange pink with little or no streaking except on the flanks and sides of the lower breast : females usually have the pink confined to the throat with sparse streaking on the upper breast as well as the lower breast and flanks. The hind claw medium or long, weak and comparatively straight. The first three primaries longest, the fourth between ·5 and 2 mm. shorter than the third : the second and third primaries emarginated, the fourth usually only slightly so. Tail pattern slightly off white, the pattern on the second outermost rectrix confined to a small triangle at the tip, rarely extending more than 10 mm. up the shaft.

The Red-throated Pipit has a complete moult of body plumage between January and April into the distinctive breeding dress.

The juvenile plumage is similar to that of the adult female in autumn without pink on the throat, but more rufous brown above with the streaks below longer and less clearly defined.

Range.—Breeds in northern Europe and Asia from Scandinavia, north of lat. 67° N., to north-eastern Siberia, and occasionally to Alaska. Winters in Africa south to southern Nigeria, the Belgian Congo and Tanganyika, occasionally in Arabia, the Maldive and Andaman Islands, Burma, Siam, Indo-China, Celebes, Borneo and the Philippines, but not in the greater part of peninsular India.

Geographical variation.—Some slight differences have been noted between the eastern and western breeding populations. The eastern birds are slightly greyer above, slightly less streaked below and average smaller (see Table 8). In addition the wing tip is usually blunter, the fourth primary being nearly equal to the third and more noticably emarginated than in western birds, in which the difference between the third and fourth is usually about 2 mm. These differences do not seem great enough to justify the recognition of two races, but the name *rufogularis* is available for western birds if required.

Identification.—Pink-throated birds are quite distinctive, the pink being richer, more orange, and less extensive on the breast than in pink-breasted specimens of *A. roseatus* and *A. spinoletta.* Young birds and some autumn females of *A. cervinus* are easily confused with *A. pratensis* and *A. trivialis* but can be distinguished by the streaked upper tail coverts, brown, rather than olive-brown, edges to the wings and feathers of the mantle, the broader white edges to the wing coverts, and heavier streaking below: *A. cervinus* has also a longer hind claw than *A. trivialis.* The Pechora Pipit, *A. gustavi*, is similar to *A. cervinus* in colour and pattern above but is smaller with a more pointed wing and a more extensive pattern on the tail; below the streaking is narrower and mostly confined to the upper breast; the bill is heavier.

11. ***Anthus gustavi***—Pechora Pipit

Specific characters.—Small. Above, brown, heavily streaked on head, mantle, rump and tail coverts, with two or three white-edged feathers to the mantle forming an indistinct V on the back: below, white or pale creamy buff, with dark, clearly defined streaks, heavy on the upper breast, rather sparse on the lower breast and flanks. The hind claw of medium length and weak. The first three primaries longest, the fourth about 4 mm. shorter than the third: the second and third primaries emarginated. The tail pattern buff or dusky white, the pattern on the second outermost rectrix usually a tapering streak extending about halfway up the shaft, but occasionally restricted to a small elongated triangle at the tip: the rectrices pointed.

The Pechora Pipit has a complete body moult between January and April into similar plumage.

The juvenile is similar to the adult except that the streaking below is less clearly defined but more extensive on the throat and abdomen.

Range.—Breeds in Eastern Europe and Siberia north of about lat. 64° N., from the Pechora region to the Bering Strait. Winters in Borneo, Timor, Celebes and Moluccas, migrating through Korea, eastern China and the Philippine Islands:

occasional stragglers travel westwards, and have been recorded at Fair Isle at different times.

Geographical variation.—Three races are recognized : the nominate race over most of the range, a slightly larger and possibly paler race, *A. g. commandorensis*, in the Commander Islands, and a darker, smaller race, *A. g. menzbieri*, breeding in south Ussuriland. The winter ranges of the respective races have not been defined but there are in the British Museum specimens which, on measurement, appear to be *commandorensis* from Celebes (♀, undated, wing 85), Labuan (unsexed, undated, wing 88) and Shaweishan (♂, May, wing 86) : also some May birds which on colour and size appear to be *menzbieri* from south China and the Philippines (wings 1 ♂ 80, 1 ♀ 74, 3 unsexed 73–79 mm.). As shown in Table 8 the few specimens available in the British Museum indicate a wider range of measurements than quoted by Johansen (1952 : 152) for the different races : his figures are quoted in brackets.

Identification.—In autumn the Pechora Pipit is easily confused with the female Red-throated Pipit. The white streaks on the mantle of *A. gustavi* have been quoted as a diagnostic character, but some white streaks are also found in *A. cervinus*, though they are not usually so pronounced or in the indistinct V pattern. Other differences between the two species have already been noted in the discussion on *A. cervinus*, and include wing formula, tail pattern and size. In winter quarters *A. gustavi* may be found in the same area as the Molucca race of Richard's Pipit, *A. novaeseelandiae medius* : this is also a small pipit but has heavy streaking above and below, with the streaks above not extending to the tail coverts, and it has a less pointed wing.

12. ***Anthus spinoletta***—Rock and Water Pipits

A. spinoletta is divided into two ecological groups of coastal and inland races. It is convenient in discussing the species to use the common name " Rock Pipit " for the coastal races of western Europe, *petrosus*, *kleinschmidti* and *littoralis*, and to use " Water Pipit " for all other races.

Specific characters.—Medium sized. Above, varying from light chocolate or deep olive brown in autumn to grey brown or grey in spring ; the streaking on head and mantle ill-defined with no sharp contrast between the feather centres and the paler edges : below, dusky white or buffish, usually suffused with pink in spring in variable degree : in autumn extensively streaked often on the abdomen as well as the breast, but the streaking ill-defined and often light in colour : in spring the streaking sparse or absent except in some Rock Pipits which have no distinctive spring plumage. The hind claw of medium length, weak and usually rather curved : the legs dark except in young birds and some from eastern Asia. The first four primaries longest and sub-equal : the second, third and fourth emarginated. The tail pattern clear white in Water Pipits, dusky in Rock Pipits : in Water Pipits from Europe and western Asia the pattern on the second outermost rectrix is usually confined to a small triangle near the tip, but is more extensive in those from eastern Europe and America : in Rock Pipits it is a mere speck at the tip or so dusky as to be indistinguishable.

Most of the races of both Rock and Water Pipits have a body moult between January and April into distinctive breeding dress, but Mayaud (1952) has shown that this moult is absent or incomplete in Rock Pipits of Britain, coastal France and the Atlantic islands.

The juvenile is similar to the adult in autumn except for the paler legs. It is a plainer, more chocolate brown above than other young pipits.

Range.—Widespread in the Northern Hemisphere. The Rock Pipits breed on the coasts of western Britain, northern France, the Faroe islands and Scandinavia, the northern birds migrating south in autumn, sometimes as far as Portugal and Italy but more usually to Britain and France. The Water Pipits breed inland in the mountains of Europe and Asia Minor, Turkestan, northwards and eastwards to Mongolia and the Bering Sea, across North America north of lat. 48° N. to western Greenland, also in the Rocky Mts. south to California. All populations move south in autumn reaching the Mediterranean, Egypt, Arabia, northern India, northern Burma, Tonkin and the Gulf of Mexico. Stragglers have occured at even more widespread localities.

A single juvenile specimen in the British Museum (No. 98.10.20.749), previously identified as another species, was collected in the valley of the Yenisei at lat. 61°.30′ N. on 8th August 1877. This represents an extension of the range of the species as shown by Dementiev and Ghladkov (1954 : Map 121). The similarity in colour of this specimen to young birds from North America suggests that it is probably *A. s. japonicus*, which is closely allied to the American races, rather than the paler *A. s. blakistoni*.

Geographical variation.—The Rock Pipits are more olive-brown than the Water Pipits, this being particularly noticeable on the rump : below the streaking is more extensive and the underparts are more washed with yellow-buff : the tail pattern is dusky rather than pure white. Within this group there is a cline from the largest, darkest and most heavily streaked race, *kleinschmidti*, in the Faroes and Hebrides, to the less richly coloured race, *petrosus*, of Wales, Ireland, England and France, and the shorter billed, paler race, *littoralis*, of Scandinavia. The most striking variation in these populations is caused, however, by the degree of moult in the body plumage that takes place from January onwards. In *kleinschmidti* and *petrosus* there is little or no winter moult so that spring birds are still dark and heavily streaked : in *littoralis* there is a fairly extensive winter moult varying individually but giving all birds a distinctive breeding dress with usually some pink on the breast, less streaking and a greyer back. Mayaud has noted that a fairly complete moult is sometimes found also in birds of the population of *petrosus* breeding on Ushant, giving them a *littoralis*-like appearance in spring. It is probable that there is some mixing of *littoralis* with this population since large numbers of Scandinavian birds winter on the coasts of northern France and a few, possibly birds coming early into breeding condition, may settle with the residents. There is also from Ushant an apparently aberrent male bird in the Meinertzhagen collection (cited as the co-type of *A. s. ponens*) collected 23rd September 1933, which is in fresh plumage similar to *littoralis* in spring. In autumn plumage most individual specimens cannot be named with certainty, but from series it is apparent that the majority of Rock Pipits wintering on the eastern and southern coasts of Britain are migrants from Scandinavia, since there are few amongst them with bills of 19 mm. which are common in *petrosus* but not found in *littoralis*. An occasional very dark, large specimen can be identified with some confidence as *kleinschmidti*.

A number of names have been given to intermediate populations which do not seem sufficiently distinct to warrant recognition on available material.

Opinions differ on the races to be recognized among the Asiatic populations of the Water Pipits, and I am more in agreement with the ranges and races recognized by Dementiev and Ghladkov (1954 : map 121) than with Vaurie. *A. s. spinoletta* of Europe is a fairly lightly streaked race with a pale pink flush in spring : the breeding birds of central Asia and China, *A. s. blakistoni*, are paler in all plumages : wintering birds of Egypt, to which the name *coutelli* was given, average smaller and have the streaking above more pronounced than either *spinoletta* or *blakistoni* ; the marks on the breast in autumn are less streaky more spotty than *spinoletta* and slightly heavier than *blakistoni*, and the rest of the underparts are washed with pale orange buff ; in spring the pink wash is warmer and more orange in tone than in either of the other two races. *A. s. coutelli* is believed to breed in the Caucasus and Persia. It seems useful therefore to retain the two names, *coutelli* and *blakistoni*, to indicate the extremes of what is probably a cline across Asia. Winter birds are hard to identify but throughout Persia, Afghanistan and north-western India the few that can be named either on size or colour are mostly *blakistoni*. However in Sind and United Provinces birds that are too small for *blakistoni* are common : those in spring plumage are near in colour to *coutelli*. Some of these are exceptionally small, even for *coutelli*, and it is possible that they belong to an unlocated breeding population in the Himalayas east of the range of typical *coutelli*. The lowest dimensions of these exceptional birds are included in brackets with *coutelli* in Table 9.

The most eastern Asiatic race, *A. s. japonicus*, is more distinctive than the other two. It breeds in eastern Siberia, possibly intergrading with American races in the extreme north-east, and migrates chiefly to China and Japan with some stragglers coming westwards to India and Burma. It is a dark race, with black, well-defined spots on the breast which are extensive in autumn but also present, though sparse, in spring : the wash on the underparts in spring is orange buff rather than pink : the legs are paler than in other races and the white in the tail often more extensive.

Three American races are now recognized, the paler *pacificus* from the west, the darker *rubescens* from the east, and a mountain population in Colorado, *alticola*, said to have a richer spring plumage. All these are fairly close to *japonicus* but differ in autumn in being a warmer brown above with less pronounced streaking, and having the spots on the breast less clearly defined and browner : in spring they are plainer in series, greyer and darker above ; below the streaking is much reduced or absent : the white in the tail is usually extensive, as in *japonicus*, but the legs are dark as in all other races. Vaurie believed that *harmsi*, based on migrants taken in Turkestan, should be considered a synonym of *rubescens*, since a co-type matched American birds. He has kindly sent me the specimen of Zarudny's on which this opinion was based. While I do not consider one can be dogmatic on single specimens, to me this bird matches rather better with a series of *japonicus* than with American birds. I would recommend that *harmsi* is transferred to the synonymy of *japonicus*, as this move has the added advantage of eliminating any question of whether or not *harmsi* should be used instead of *pacificus*, which it antedates, for the western American birds, now that *rubescens* is confined to the eastern populations.

Identification.—The differences between the two ecological groups of Rock and Water Pipits have been discussed under geographical variation. The species as a whole is unlikely to be confused with other pipits though in size and plumage variations it appears to be closely related to the greenish *A. roseatus*. The dark, comparatively unstreaked back, and dark legs combined with the extensive but ill-defined streaking or pale pink underparts of most races are quite distinctive. *A. s. japonicus* is more like *A. trivialis* and *A. pratensis* below than the other Palaearctic races, but has different dimensions and is greyer and less streaked above.

MEASUREMENTS OF SPECIES IN GROUP A

(based on a minimum of 15 ♂ 15 ♀ unless otherwise stated)

TABLE 2.—*Australian, Melanesian and Philippine Forms of A. novaeseelandiae* (pp. 253–254)

	Wing		Bill		Tail*		Hind claw	Tarsus ♂♀
	♂	♀	♂	♀	♂	♀		
All New Zealand races, 7 ♂, 6 ♀	89–99	84–90	16–18	16–17·5	67–72	63–68	11–13	23–26
steindachneri, 1 ♂, 2 ♀	87	86–87	20	18–19	61	57	12–13	24–26
aucklandicus, 3 ♂, 1 ♀	86–89	91	18–23	19	59–65	68	12–17	24–26
All Australian races, 12 ♂, 9 ♀	86–95	79–85	16–18	16–17	56–67	53–60	9–13	23–28
exiguus, 3 ♂, 4 ♀	85–87	77–83	17–18	16·5–18	57–60	52–56	10–12	25–27
medius, 5 ♂, 4 ♀	79–80	77–80	17–17·5	17–18	51–55	55–56	10–12	24–26
albidus, 2 ♂, 1 ♀	80	77	17	18	56–57	54	11	25–26
lugubris	78–83	75–79	17–18	16·5–18	52–58	51–55	12–19	27–29

* See p. 249.

TABLE 3.—*Asiatic Mainland, and Palaearctic Races of A. novaeseelandiae* (pp. 254–256)

	Wing		Bill		Tail*		Hind claw	Tarsus ♂♀
	♂	♀	♂	♀	♂	♀		
richardi (breeding), 7 ♂, 2 ♀	91–99 (101)	93–94	18·5–19	18–19	64–72	71	15–20	29–33
centralasiae (breeding), 4 ♂, 1 ♀	98–100 (96–102)	92	18–21	18·5	69–73	66	15–22	30–33
dauricus (breeding), 3 ♂, 2 ♀	90–96	87–92	18–19	17·5–18·5	63–69	64–69	14–19	28–31
ussuriensis (breeding), 5 ♂	90–95	—	18–19	—	63–70	—	15–18	30–31
richardi subspp. (all year)	90–102	87–94	18–21	17–19	63–73	62–71	14–22	28–33
sinensis (breeding), 8 ♂, 8 ♀	87–91	81–88	17–18	16·5–18	58–64	55–62	12–19	27–30
Annam pop. (breeding), 6 ♂, 5 ♀	80–90	80–86	16·5–17	16–17·5	57–62	54–59	10–18	26–29
malayensis, *rufulus*, and *waitei*	77–87	74–83	16–18	15–18	51–61	49–56	10–18	24–28

* See p. 249.

TABLE 4.—*African Races of A. novaeseelandiae* (pp. 256–258)

	Wing		Bill		Tail*		Hind claw	Tarsus ♂♀
	♂	♀	♂	♀	♂	♀		
cinnamomeus	82–97	79–91	16–18·5	16–18	55–65	53–65	11–17	24–29
bocagei	84–93	77–86	17–18·5	16–17	55–66	52–60	9–15	24–28
rufuloides	87–94	84–93	16–18	16–17	59–64	57–61	11–15	24–28
lwenarum, 4 ♂, 1 ♀	93–95	97	17–19	19	65	67	11–13	28
editus, 3 ♂, 2 ♀	94–97	88–89	17·5–18	17	63–65	62–64	13–15	26–29
hoeschi, 1 ♀ (type)	—	96	—	17	—	—	14	29
cameroonensis, 4 ♂, 2 ♀	91–95	93–95	17–19	18	57–68	64–65	9–11	26–28
lynesi, 4 ♂, 3 ♀	95–99	90–92	17–18	17–18	65–71	63–66	9–10	25–27

* See p. 249.

TABLE 5.—*Anthus godlewskii and A. campestris* (pp. 258–260)

	Wing		Bill		Tail*		Hind claw	Tarsus ♂♀
	♂	♀	♂	♀	♂	♀		
A. godlewskii	90–97	84–93	16·5–18	16–17·5	62–70	59–64	11–15	24–28
A. c. campestris	88–101	82–91	18·5–20	17–20	61–67	59–66	9–14	24–28
A. c. kastschenkoi	85–90	80–87	17–18	16–17	55–65	54–61	8–13	23–26

* See p. 249.

TABLE. 6.—*Races and Populations of Anthus similis* (pp. 261–262)

	Wing		Bill		Tail*		Hind claw	Tarsus ♂♀
	♂	♀	♂	♀	♂	♀		
similis, travancoriensis, 7 ♂, 2 ♀	90–96	89–90	19–21	19	72–76	70–72	9–11	26–28
yamethini, 8 ♂, 4 ♀	87–92	84–89	18–19	18	67–73	66–67	8–11	24–26
decaptus, jerdoni	94–105	92–99	19–21	18–21	71–82	69–82	9–14	26–29
captus, arabicus	90–98	86–92	18–20	17–20	68–72	62–70	8–13	23–26
nivescens, jebelmarrae, asbenaicus, hararensis, hallae, nyassae	88–103	87–100	17–20	17–20	57–75	58–71	8–11	24–28
schoutedeni, 10 ♂, 3 ♀	86–97	85–92	15–17	15–17	57–65	58–60	8–10	23–25
nicholsoni and *leucocraspedon*	91–102	87–96	17–21	17–20	64–72	58–72	9–14	24–28
bannermani and *josensis*, 3 ♂	85–86	—	17–18	—	60–64	—	7–10	24–25
sokotrae, 15 specimens	82–91		19–22		56–71		10–11	24–26

* See p. 249.

TABLE 7. *Anthus vaalensis, A. leucophrys and A. palidiventris* (pp. 262–266)

	Wing		Bill		Tail*		Hind claw	Tarsus ♂♀
	♂	♀	♂	♀	♂	♀		
Southern Africa								
A. v. vaalensis and *daviesi*, 15 ♂, 10 ♀	101–111	92–103	18–20	17–19	67–76	68–75	8–12	28–32
A. v. neumanni and *chobiensis*	92–105	89–102	17–20	16–20	62–73	59–69	8–13	26–30
A. l. leucophrys . . .	89–102	89–99	17–18·5	16–18	58–66	55–66	11–17	27–31
A. l. bohndorffi . . .	95–102	89–97	17–19	16–18·5	60–71	58–64	12–17	27–31
Northern Africa								
A. l. saphiroi, 12 ♂, 10 ♀ .	90–101	90–97	17–18	15–17·5	61–67	60–67	10–12	24–28
A. l. goodsoni, 3 ♂, 7 ♀ .	99–102	93–99	17	16·5–18	65–70	63–66	10–12	27–29
A. l. omoensis, 13 ♂, 8 ♀ .	98–108	97–102	17–19	17–18·5	65–71	67–70	10–18	26–30
A. l. zenkeri . . .	89–101	85–97	16–18·5	16–18·5	59–69	58–68	9–18	24–29
A. l. ansorgei, 9 ♂, 9 ♀ .	90–95	85–95	17–19	17–18	65–69	59–66	9–12	23–28
A. l. gouldi, 11 ♂, 4 ♀ .	86–96	88–89	17–19	17–18·5	58–69	60–65	9–14	25–27
A. p. pallidiventris, 4 ♂, 3 ♀	95–99	93–96	19–20	19–20	61–64	55–59	13–16	31–33
A. p. esobe, 2 ♂, 1 ♀ . .	96–97	91	19–20	19	59	56	13–16	31–32

* See p. 249.

TABLE 8.—*Anthus pratensis, A, trivialis, A. hodgsoni, A. roseatus, A. cervinus, A. gustavi* (pp. 266–272)

	Wing		Bill		Tail*		Hind claw	Tarsus ♂♀
	♂	♀	♂	♀	♂	♀		
A. pratensis	77–85	73–83	14–16	14–15	51–58	49–56	9–15	20–23
A. t. trivialis . . .	84–95	80–90	14–16	14–16	50–61	51–59	8–10	20–23
A. t. sibirica, 15 ♂, 8 ♀ .	81–88	79–85	13–15	14–15	52–57	52–57	8–10	20–21
A. t. haringtoni, 12 ♂, 6 ♀ .	84–89	83–87	14–15	14–15	54–60	54–58	7–9	20–22
A. h. hodgsoni (typical) .	79–86	77–85	13–16	14–16	53–61	50–59	8–9	20–22
A. h. hodgsoni (Japan, see p. 000) 10 ♂, 7 ♀ 18 unsexed	81–86 (81–87)	81–83	15–16·5 (15–16·5)	15–16	51–55 (47–54)	50–53	8–9	20–22
A. h. yunnanensis . .	81–90	77–83	14–16	14–15	51–61	52–56	8–9	20–21
A. roseatus	86–92	79–87	15–17	15–16	57–62	52–58	10–14	22–24
A. cervinus, Europe and W. Siberia	83–90	80–87	14–16	14–15	49–56	47–55	9–13	20–22
A. cervinus, E. Siberia, 5 ♂, 5 ♀	83–85	79–83	14–15	14–15	51–55	48–51	9–13	21–22
A. g. gustavi, breeding 8 ♂ 6 ♀	81–86 (82–84)	77–82 (78–81)	16·5–17	15–16·5	47–51	47–51	10–13	20–22
A. g. commandorensis, breeding, 3 ♂, 1 ♀	86–89 (83–86)	85 (79–83)	16–17	16	51–55	55	10–13	24–26
A. g. menzbieri (winter), 1 ♂, 1 ♀, 3 unsexed	80 (76–79)	74 (73–77)	16 (15)	16	51 (45–46)	46	10–12	21–23

* See p. 249.

TABLE 9.—*Races and Populations of Anthus spinoletta* (pp. 272–275)

	Wing		Bill		Tail*		Hind claw	Tarsus ♂♀
	♂	♀	♂	♀	♂	♀		
Rock Pipits								
kleinschmidti (Faroes and Outer Hebrides)	88–95	83–89	18–19	19	58–62	58–59	11–12	23–25
petrosus (England, Wales, Ireland)	88–94	83–90	17–19	18–20	55–64	52–60	8–14	22–25
littoralis (Scandinavia)	87–93	80–87	16·5–18	16·5–18	56–60	51–56	9–14	23–25
Water Pipits								
spinoletta	88–95	80–89	16–18	15–17	57–63	54–60	10–14	22–24
coutelli (Egypt and Cyprus, 5 ♂, 9 ♀, and N. India, see p. 274)	85–92 (83)	80–87	16–17	16–17 (15)	55–61 (54)	54–59 (52)	10–13	23–25
blakistoni	88–96	83–90	16–18	16–18	59–66	56–61	9–14	23–24
japonicus	86–91	79–88	15–17	15–17	54–62	53–60	10–14	22–25
pacificus and *rubescens*	80–90	78–86	14–17	14–16	55–64	53–57	9–13	22–24

* See p. 249.

GROUP B. DISTINCTIVE ASIAN, AFRICAN AND AUSTRALASIAN SPECIES

None of the species in this group presents difficulty in identification to any student with an appropriate regional handbook, since all have distinctive characters, many have very restricted ranges, and none is a true migrant. They have therefore not been illustrated: their characters have been summarized with particular reference to their distinctive characteristics: the range and any geographical variation is outlined: as a guide to general size measurements have been given of specimens available although in some of the rarer species the series is not adequate to show the full range of size.

ASIAN SPECIES

Anthus nilghiriensis—Nilgiri Pipit

Confined to high altitudes in the Nilgiri and Palni Hills of southern India, rarely descending to the plains.

A medium sized pipit with short, blunt wings and a short bill. Above, rich tawny brown, heavily streaked on head and mantle: below, rich buff, distinctly but sparsely spotted on the upper breast with small spots and lightly streaked on the lower breast and flanks. The hind claw of medium length and curved. The first four primaries sub-equal with the fifth only 1–2 mm. shorter: the second to fifth emarginated. The rectrices rather pointed, with the pattern buff: the pattern on the second outermost a tapering triangle up the shaft, and the third outermost having a small triangle at the tip. Measurements of 16 ♂ 11 ♀: wing ♂ 76–80, ♀ 73–78: bill ♂ 15–16, ♀ 14–16: tail ♂ 53–61, ♀ 52–60: hind claw ♂ ♀ 9–13: tarsus ♂ ♀ 24–25.

The well-defined streaking, short, blunt wing and extensive patterning on the tail combine to distinguish the Nilgiri Pipit from all others likely to be found in the area.

Anthus sylvanus—Upland Pipit

Confined to the mountains of central Asia from Afghanistan to Yunnan and eastern Sikang, rarely descending to the plains.

A large pipit with short, blunt wings and a short heavy bill. Above, light pinkish brown, heavily streaked on head, mantle, rump and tail coverts with dark brown: below, pale buff or white, streaked with fine hair-streaks on the lower breast, flanks and abdomen: these streaks are wider on the flanks and those on the breast divide at the tip of the feather forming a small triangle. The hind claw short and strongly curved. The first four primaries sub-equal with the fifth only 1–3 mm. shorter: the second to fifth emarginated. The rectrices narrow and very pointed with the tail pattern dusky and the same triangular pattern as in *A. nilghiriensis* on the second and third outermost. Measurements 22 ♂ 10 ♀: wing ♂ 78–84, ♀ 74–80: bill ♂ ♀ 16–18: tail ♂ 59–69, ♀ 56–63: hind claw ♂ ♀ 8–11: tarsus ♂ ♀ 24–25.

There is a cline from paler birds, *A. s. oreinus*, in the west, to darker birds, *A. s. sylvanus*, in the east.

The fine hair-streaks on the abdomen, heavy bill and pointed rectrices distinguish the Upland Pipit from all others, but it can be seen that in the shape of the wing, the pattern of the tail and conformation of the hind claw, it has many points of similarity with the Nilgiri Pipit, which replaces it in the mountains of southern India.

AFRICAN SPECIES

Anthus berthelotii—Berthelot's Pipit

Confined to the Canary Islands and Madeira.

A small pipit with a long bill. Above, dark brown, the streaking on the head and mantle therefore not very distinct: below, white, with distinct spotting on the upper breast and sparse streaks on the sides of the lower breast and flanks. The hind claw fairly long and straight. The first four primaries sub-equal with the fifth about 6 mm. shorter: the second to fourth emarginated. The tail pattern white with the pattern on the second outermost rectrix, as in *A. campestris*, usually extending up the shaft in a tapering streak, sometimes reduced to a short streak near the tip. Measurements of 35 ♂ 22 ♀: wing ♂ ♀ 69–79, bill, Canary Is. ♂ 15–17, ♀ 14–16, Madeira ♂ 16–18, ♀ 16–17: tail ♂ ♀ 48–56: hind claw ♂ ♀ 8–16; tarsus ♂ ♀ 23–24.

Birds of Madeira have rather longer bills than those of the Canary Islands and have been separated as *A. b. madeirensis*. It has been suggested that there is some variation in colour between the populations of other islands but sufficiently good series of fresh plumaged birds are not available on which to establish this.

Size alone distinguishes Berthelot's Pipit from any of the Palaearctic migrants that might visit the islands. On field characters and voice it has been shown by Lack and Southern (1949: 619) and Volsøe (1951: 106) that this species has affinities with the Tawny Pipit, *A. campestris*. Morphologically there is little to suggest closer affinities with *A. campestris* than with some other species, the associations being dependent on which characters are selected as being of most importance: the similarity of hind claw, tail pattern and wing formula between *A. berthelotii* and *A. campestris* are offset by the considerable differences in pattern, colour, size, and in the lack of a spring moult.

Anthus lineiventris—Striped Pipit

Found throughout most of Africa south of the Equator.

A large pipit with green edges to the wings. Above, dark brown, with heavy but indistinct streaking on head, mantle, rump and tail coverts; the wings and tail edged with green: below, creamy white, extensively streaked from the upper breast to the tail coverts with well-defined dark brown streaks. The hind claw short, curved and strong. The wing blunt, the first four primaries sub-equal and the fifth only 1–3 mm. shorter: the second to fifth emarginated. The tail pattern clear white and in the form of triangles of diminishing size on the inner webs of the three outermost rectrices. Measurements of 25 ♂ 22 ♀: wing ♂ 85–90, ♀ 82–88: bill ♂ ♀ 18–20: tail ♂ ♀ 59-68, ♀ 58-64: hind claw ♂ ♀ 9–10: tarsus ♂ ♀ 28–30.

The green edges to the wings and tail, combined with the extensive streaking below, make the Striped Pipit quite distinctive among African pipits, though with a superficial resemblance to the Palaearctic *A. roseatus* in autumn.

Anthus brachyurus—Short-tailed Pipit

Sporadically distributed from Kenya to Angola and Natal.

A miniature, dark pipit. Above dark brown, with heavy but indistinct streaking on head and mantle. Below creamy-white on the breast, with heavy, well-defined, short streaks; white on the abdomen and flanks with very sparse fine streaks. The hind claw short and curved. The wing blunt, the first four primaries sub-equal and the fifth 1–3 mm. shorter: the second to fourth emarginated. The tail pattern dusky white on the outer rectrix and absent from or very small, on the second outermost. Measurements of 12 ♂ 12 ♀: wing ♂ 64–68, ♀ 60–65: bill ♂ 13–14, ♀ 12–13: tail ♂ 33–39, ♀ 32–36: hind claw ♂ ♀ 7: tarsus ♂ ♀ 16–18.

Northern birds, *A. b. leggei*, are alleged to be smaller and darker than the southern, *A. b. brachyurus*. The differences are just apparent but not very convincing and it seems impossible to make a clear division between the ranges of the two races.

The Short-tailed Pipit is the smallest Old World Pipit: the only other small pipits found in Africa are the following species, *A. caffer* and *A. sokokensis*, which are a richer brown with longer tails.

Anthus caffer—Little Tawny Pipit

Sporadically distributed from southern Abyssinia to Angola and the Transvaal.

A small pipit with a misleading name since it is richer and less sandy in colour than the Tawny Pipit. Above, light brown, heavily and distinctly streaked on head and mantle: below, white, with dark brown streaks on the breast. The hind claw short and curved. The wing blunt, the first four primaries sub-equal, the fifth 2-4 mm. shorter; the second to fourth emarginated and the fifth slightly so. The tail pattern usually clear white, with a small spot or triangle on the second outermost rectrix: the pattern in Abyssinian birds is buffish and sometimes extends as a short streak up the shaft. Measurements of 8 ♂ 8 ♀: wing ♂ 67–77, ♀ 67–75: bill ♂ ♀ 12–16: tail ♂ ♀ 41–51: hind claw ♂ ♀ 6–8: tarsus ♂ ♀ 17–19.

Four races are recognized on slight differences of size and colour, *A. c. caffer* of southern Africa and *A. c. mzimbaensis* of Nyasaland being slightly larger and longer billed than *A. c. australoabyssinicus* of Abyssinia and the paler *A. c. blayneyi* of Tanganyika.

The Little Tawny Pipit is richer coloured and longer tailed than the Short-tailed Pipit, with the richer brown above particularly noticeable on the rump in contrast to the dark, almost blackish rump of *A. brachyurus.*

It is similar in many respects to the next species, *A. sokokensis* which, in parts of East Africa, occurs in the same area, though not in the same type of country, but which is less rich in colour above, has a different pattern on the breast and lacks the pointed rectrices of *A. sokokensis.* Their relationship will be discussed later.

Anthus sokokensis—Sokoke Pipit

Confined to woodland clearings associated with surviving patches of forest in the Sokoke forest near Mombasa, Moa at sea level one hundred miles south, and the Pugu Hills near Dar-es-Salaam.

A small, richly coloured pipit with pointed rectrices. Above, rich orange brown, with broad, dark streaks on head and mantle and light streaks on the rump and upper tail coverts: below, creamy white, with large blotchy black spots confined to the upper breast. Hind claw short and rather straight. The wing blunt, the first four primaries sub-equal and the fifth only about 1 mm. shorter: the second to fourth emarginated, the fifth slightly so. The rectrices pointed with the pattern clear white, with a small, elongated triangle on the second outermost rectrix. Measurements of 1 ♂ 2 ♀: wing ♂ ♀ 68–69: bill ♂ 16, ♀ 15: tail ♂ 49, ♀ 46: hind claw ♂ ♀ 7–8: tarsus ♂ ♀ 18–19.

The similarity between the Sokoke Pipit and the Little Tawny Pipit can be appreciated by comparison of the descriptions and measurements. The chief differences lie in the richer colour above of the Sokoke Pipit, the different pattern on the breast and the shape of the tail feathers: they are similar in size and the general extent of the pattern above and below, and in the wing formula and tail pattern. It seems likely that *A. sokokensis* and *A. caffer* are derived from the same stock but have diverged in different environments.

Anthus melindae—Malindi Pipit

Confined to coastal Kenya.

A medium sized, plain backed pipit. Above, plain brown: below, white, with extensive light brown streaks on the breast extending sparsely to the abdomen and flanks. The hind claw of medium length and fairly straight. The wing blunt, the first four primaries sub-equal with the fifth about 3 mm. shorter: the second to fifth emarginated. The tail pattern dusky white on the outermost rectrix and absent from the second outermost in the few specimens examined. Measurements of 4 ♂ 1 ♀; wing ♂ ♀ 83–86: bill ♂ ♀ 16–17: tail ♂ ♀ 48–56: hind claw ♂ ♀ 10–11: tarsus ♂ ♀ 25–27.

The combination of the plain back and the extensive brown streaking below distinguish the Malindi Pipit from all others. It is also smaller than the Plain-backed Pipits of the *A. leucophrys/vaalensis* group and larger than *A. brachyurus*, the only other African pipit with a plain back.

Anthus chloris—Yellow-breasted Pipit

Confined to the south-eastern districts of South Africa.

A medium sized pipit with some bright yellow on the underparts. Above, light brown, heavily streaked on the head and scalloped rather than streaked on the mantle with very dark brown : below, in breeding dress, lemon yellow from the throat to the upper abdomen, with little or no streaking on the breast ; in non-breeding dress the yellow replaced by tawny buff except for a yellow patch on the upper abdomen. Hind claw long and weak. The wing blunt, the first four primaries sub-equal, the fifth less than 2 mm. shorter : the second to fifth emarginated. The tail pattern clear white with a small, elongated triangle on the second outermost rectrix and a spot on the third. Measurements of 8 ♂ 5 ♀ : wing ♂ 85–91, ♀ 82–85 : bill ♂ 17–18 : tail ♂ 60–65, ♀ 56–59 : hind claw ♂ ♀ 12–17 : tarsus ♂ ♀ 24–27.

In colour and pattern the Yellow-breasted Pipit is distinct from all other members of the genus *Anthus*. It has the appearance of a minature Longclaw but lacks the rictal bristles that are considered a generic character of *Macronyx*. Birds in non-breeding dress bear a superficial resemblance to the female Golden Pipit, *Tmetothylacus tenellus*, but the Golden Pipit is easily distinguished by its yellow tail pattern and less richly coloured mantle. The two species are not normally found together since the Golden Pipit is primarily an East African species but there is one unsubstantiated record of its occurrence in the Transvaal.

Anthus crenatus—Cape Rock Pipit

Confined to hills and mountains from southern and eastern Cape Province to Pondoland and eastern Transvaal.

A large almost plain, pipit with greenish edges to the wing, and rich buff underparts. Above, brown with faint streaks on head and mantle, a yellow-green shoulder and greenish edges to the wing : below, the throat white, the rest of the underparts light tawny brown with very faint streaking on the breast : axillaries yellow. The hand claw short and strongly curved. The wing blunt, the first five primaries sub-equal ; the second to fifth emarginated. The tail pattern buff, very reduced on the outermost rectrix and limited to a small spot at the tip of the second. Measurements of 5 ♂ 3 ♀ : wing ♂ 88-91, ♀ 83–86 : bill ♂ ♀ 19–21 : tail ♂ 56–61, ♀ 56–58 : hind claw ♂ ♀ 10–12 : tarsus ♂ ♀ 28–29.

The Cape Rock Pipit has a rather stocky build, heavy legs and bill giving an un-pipit-like appearance, though it has some features in common with *A. similis*. It is easily distinguished from the sympatric *A. similis nicholsoni* by the greenish edges to the wing, yellow shoulder and axillaries, and the plainer pattern above and below.

AUSTRALASIAN SPECIES

Anthus gutturalis—New Guinea Pipit

Confined to the mountains of New Guinea.

A large, dark pipit. Above, dark brown, with indistinct streaks on head and mantle: below, the throat yellow buff constrasting with pale sepia brown on the breast which merges into yellow buff on the abdomen; the breast unspotted except in young birds. The hind claw short and strongly curved. The wing blunt with the second, third and fourth primaries sub-equal and the first and fifth about 2–3 mm. shorter: the second to fifth emarginated. The tail pattern very dusky and limited on the second outermost rectrix to a small triangle at the tip. Measurements of 6 ♂ 5 ♀: wing ♂ 99–102, ♀ 93–98: bill ♂ ♀ 17–18: tail ♂ 64–77, ♀ 64–73: hind claw ♂ ♀ 8–10; tarsus ♂ ♀ 27–30.

Three races are recognized on slight differences of colour and size.

The New Guinea Pipit in its heavy structure is another un-pipit-like member of the genus, but closest to the Cape Rock Pipit, *A. crenatus*, and *A. similis*. Its structure and the brown, unstreaked underparts distinguish it from the other resident pipit of New Guinea, *A. novaeseelandiae exiguus*, and from any likely migrants.

GROUP C. AMERICAN AND SOUTH ATLANTIC SPECIES

American species are poorly represented in the British Museum and it has not therefore been possible to make a detailed study of them. However it seems useful to list their characters under the same formula as has been used for the Old World pipits so that comparisons can be made easily between them. On the whole I do not find it possible to associate many American species directly with those of the Old World, especially without knowledge of their field characters, but I have noted a few instances in which there seems some relationship. As with species of Group B, members of this group have not been illustrated and the measurements, taken mostly from inadequate samples, are provided only to give indication of the relative sizes. It has not been possible to assess the degree of individual and geographical variation or the ranges of the races. Hellmayr (1935) and Zimmer (1953) have been followed.

Anthus spragueii

The only endemic North American pipit: breeding in the central plains from eastern Montana to Manitoba, migrating as far south as Mexico.

A medium sized, rather light-coloured pipit. Above, tawny brown, with broad but not very dark streaks on head and mantle: below, white on the abdomen, pale buff on the breast and throat, lightly and sparsely streaked on the upper breast with well-defined short streaks. The hind claw medium to long, rather weak and sometimes rather straight. The first four primaries sub-equal with the fifth about 8 mm. shorter: the second to fourth emarginated. The rectrices slightly pointed, with the pattern pure white extending in a long narrow streak up the shaft on the second outermost rectrix. Measurements of 10 ♂ 5 ♀: wing ♂ 81–85, ♀ 79–82: bill ♂ ♀ 14–15: tail ♂ 51–57, ♀ 50–53: hind claw ♂ ♀ 10–14: tarsus ♂ ♀ 22–24.

Morphologically I can see no reason to consider *A. spragueii* specifically distinct from the following species, *A. furcatus*, of South America. The only differences between them are in the degree of marking on the breast and a slight difference in the size of the leg and foot as indicated by the length of the tarsus. Unless significant differences can be demonstrated in their field characters, I would recommend that Sprague's Pipit be considered a race of *A. furcatus*. In structure the two forms appear to be the New World representatives of the *A. campestris/godlewskii/berthelotii* complex, but I cannot speak for their field characters.

Anthus furcatus

Confined to central South America from Peru and Bolivia south to Uruguay.

Similar in all characters to *A. spragueii* except that the buff of the upper breast and throat is slightly darker and the streaks on the breast are broader, forming brown, rather heavy, spots, instead of the narrow, short streaks. Measurements of 8 ♂ 19 ♀: wing ♂ 77–85, ♀ 74–80: bill ♂ ♀ 13–15: tail ♂ 48–55, ♀ 48–52: hind claw ♂ ♀ 8–13: tarsus ♂ ♀ 20–22.

Birds from Peru and Bolivia have been separated as *A. f. brevirostris* and can be distinguished by slight differences in colour and size.

Anthus lutescens—(*A. chii* of Zimmer)

Widespread in South America from Panama to northern Chile, Argentine and Paraguay.

A miniature pipit. Above, dark brown, heavily streaked on head, mantle, rump and tail coverts: below, pale lemon yellow, with brown indistinct spotting confined to the upper breast. Hind claw long and rather straight. The first four primaries sub-equal with the fifth 4–6 mm. shorter: the second to fourth emarginated. The tail pattern clear white, with the pattern extending in a long narrow streak up the shaft on the second outermost rectrix. Measurements of 18 ♂ 19 ♀: wing ♂ 60–70, ♀ 59–69: bill ♂ ♀ 13–15: tail ♂ ♀ 39–46: hind claw ♂ ♀ 9–15: tarsus ♂ ♀ 19–21.

Zimmer recognizes four races on slight differences of colour, *A. l. parvus* from Panama, *A. l. abariensis* from the north of South America, *A. l. peruvianus*, from Peru and northern Chile, and *A. l. lutescens* from central South America.

It is tempting to associate *A. lutescens* with the miniature pipits of Africa, in particular with the dark *A. brachyurus*, but, in fact, the two species have little in common except their small size and dark appearance.

Anthus chacoensis

Confined to Argentine and Paraguay.

Similar to *A. lutescens*, except that the streaking above and below is more clearly defined and extends to the sides of the lower breast and flanks: the underparts are whiter: the hind claw is short (7–8 mm.): the pattern on the second outermost rectrix is restricted to a small spot at the tip. Measurements of 1 ♀: wing 65: bill 13: tail 44: hind claw 8: tarsus 20.

Anthus correndera

Found throughout central and southern South America from Peru and southern Brazil to Tierra del Fuego, and in the Falkland Islands.

A medium sized, heavily streaked pipit. Above, light brown, heavily streaked on head, mantle, rump and tail coverts with dark brown, and with a few white streaks in the mantle, similar to those in *A. cervinus*: below, white, heavily marked on the whole breast and flanks with large spots or broad dark brown streaks. The hind claw long, straight and weak. The first four primaries longest and sub-equal with the fifth about 2–5 mm. shorter: the second to fourth emarginated. The tail pattern is clear white, with the pattern on the second outermost rectrix varying from a long narrow streak up the shaft to a small streak at the tip. Measurements of 37 ♂ 17 ♀ from South America: wing ♂ 72–80, ♀ 71–78: bill ♂ ♀ 14–17: tail ♂ 48–57, ♀ 47–52: hind claw ♂ ♀ 10–20: tarsus ♂ ♀ 21–24. Measurements of 8 ♂ from the Falkland Islands, *A. c. grayi*: wing 80–84: bill 15–16: tail 54–57: hind claw 14–20: tarsus 22–23.

Apart from the larger *A. c. grayi* of the Falkland Is. Zimmer recognizes four races: *A. c. chilensis* of Chile and Tierra del Fuego; *A. c. correndera* from southern Argentine, Uruguay and southern Brazil; *A. c. catamarcae* from northern Argentine: and *A. c. calcaratus* from Peru. The differences are not very well marked.

The superficial resemblance in colour and pattern between some specimens of *A. correndera* and the Palaearctic *A. gustavi* is remarkable, but nevertheless I do not think the two species are closely related as there is a significant difference in the juvenile plumage as well as some differences in the hind claw, wing formula and tail pattern. In *A. gustavi* the juvenile plumage is similar in most respects to that of the adult, whereas in *A. correndera* the juvenile has white edges to the mantle feathers, giving a scalloped effect and a less brown, more black-and-white, appearance than the adult.

The length of the hind claw and the tail pattern suggest that *A. correndera* may be the American representative of *A. novaeseelandiae* though it has more streaking both above and below.

Anthus antarcticus

Confined to South Georgia.

A large pipit, with extensive streaking below. Above, brown, heavily streaked on head, mantle, rump and tail coverts with dark brown, and some whitish streaks. Below, white washed with pale buff, heavily streaked on breast and flanks, with some light streaking on throat and abdomen, heavier in young birds. The hind claw long, and very heavy and straight. The wing blunt, the first four primaries sub-equal with the fifth only 2–3 mm. shorter: the second to fourth emarginated and the fifth slightly so. The tail pattern dusky white with little or no pattern on the inner web of the second outermost rectrix. Measurements of 3 adults: wing 81–84: bill 16–19: tail 58–62: hind claw 13–17: tarsus 25–26.

A. antarcticus appears to be the representative in South Georgia of *A. correndera*, but has diverged sufficiently to be regarded as a distinct species.

Anthus nattereri

Confined to south-eastern Brazil and Paraguay.

A medium sized, richly coloured pipit. Above, rich tawny brown, heavily streaked on head and mantle, and lightly streaked on the rump and tail coverts, with dark brown: below, throat white, washed with yellow, breast and flanks washed with rich orange buff and lightly streaked with brown, abdomen white. Hind claw long, weak and straight. Wing blunt, the first four primaries sub-equal, the fifth 4 mm. shorter: the second to fifth emarginated. Rectrices narrow and pointed, with the tail pattern dusky with a long narrow streak up the shaft on the second outermost rectrix and a small spot on the tip of the third. Measurements of type only (unsexed) : wing 76 : bill 14 : tail 57 : hind claw 16 : tarsus 25.

Anthus hellmayri

Confined to central and southern South America from Peru to the Argentine and south-eastern Brazil.

A medium sized pipit, heavily streaked above, but lightly streaked below. Above, light or rich brown heavily streaked on head, mantle and rump with dark brown : below, pinkish buff, with narrow sparse streaks on the upper breast and flanks. Hind claw medium to long, rather strong and usually rather curved. The wing blunt, the first four primaries sub-equal, the fifth 1–2 mm. shorter : the second to fifth emarginated. Rectrices rather pointed with the pattern dusky white or white (*A. h. dabbenei*), and varying on the second outermost rectrix from a small spot or streak near the tip (*A. h. hellmayri*) to a narrow streak up the shaft in some specimens of *A. h. dabbenei* and *A. h. brasilianus*. Measurements of 7 specimens : wing 71–80 : bill 14–15 : tail 46–57 : hind claw 10–13 : tarsus 22–24.

Zimmer recognizes three well-marked races ; *hellmayri* from the north-west ; the paler *dabbenei* from western Argentine and the Chile border, which migrates northwards in winter ; and the richer coloured *brasilianus* from the east.

There are few records of *A. h. hellmayri* from Peru, and it therefore seems worth noting that there is a specimen in the British Museum collected at Capachica, Lake Titicaca, on 5th June 1937 by P. F. Holmes.

Anthus bogotensis

Confined to western South America from western Venezuela to north-western Argentine.

A medium sized pipit, heavily streaked above. Above, rich or light brown very heavily streaked on head, mantle, rump and tail coverts : below, light or orange buff, sparsely spotted on the upper breast and very sparsely streaked on the flanks. Hind claw medium to long, rather strong, and usually rather curved. The wing blunt, the first five primaries almost equal : the second to fifth emarginated. The tail pattern dusky usually restricted to a small spot or streak on the second outermost rectrix, but occasionally a narrow streak up the shaft. Measurements of 11 ♂ 15 ♀ : wing ♂ 80–86, ♀ 76–83 : bill ♂ ♀ 15–17 : tail ♂ 50–55, ♀ 49–55 : hind claw ♂ ♀ 9–17 : tarsus ♂ ♀ 23–25.

Zimmer recognizes four races on small differences of colour, pattern and size ; *A. b. meridae* from western Venezuela ; *A. b. bogotensis* from Colombia and Ecuador ; *A. b. immaculatus* from Peru ; and *A. b. shiptoni* from Bolivia and Argentine.

ACKNOWLEDGMENTS

Many friends have earned my gratitude for their help in the preparation of this paper but they cannot all be named. I must, however, mention particularly my indebtedness to Mr. C. M. N. White for his advice on African pipits, to Dr. Charles

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Other specimens have been borrowed from the Academy of Natural Sciences, Philadelphia, the Chicago Natural History Museum, the Musée du Congo Belge, Tervuren, the Peabody Museum, Yale University, the Royal Scottish Museum, Edinburgh, and the Zoologishes Museum, Berlin. For these I am most grateful to the Directors of the institutes concerned.

SUMMARY

Five diagnostic characters have been selected to aid in the specific recognition of pipits : colour and pattern, size, the conformation of the hind claw, the tail pattern, and the wing formula.

Variation in these characters is discussed with reference as well to some peculiarities in moults of pipits.

The difficulties of subspecific definition and recognition are discussed in relation to migration, ecological variation and clinal variation.

The pipits of the world are divided into three groups under which their characters, ranges, geographical variation and identification are summarized with some notes on the relationship between certain species. Group A includes old world species which present difficulty in identification ; these are discussed fully and illustrated in Plates 56–61 ; their measurements are listed for comparison in Tables 2–9. Group B, includes distinctive Old World and Australasian species, and Group C American and South Atlantic species : species in these groups are discussed less fully and not illustrated : the measurements of available specimens is included in the text.

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APPENDIX

Amendents proposed in this paper to the systematic list of Pipits in Check-List of Birds of the World, 9, 1960.

Anthus novaeseelandiae ussuriensis. Here recognized as a good race breeding in eastern Siberia, distinct from *A. n. sinensis* of south China.

Anthus novaeseelandiae hoeschi. Here considered as distinct from *A. n. bocagei*, and possibly will prove a good race allied to *A. n. lwenarum* and *A. n. editus.*

Anthus campestris griseus. Here considered a synonym of *A. c. campestris.*

Anthus campestris kastschenkoi. Here considered a good race breeding between the Ob and Yenisei rivers, and wintering in India.

Anthus similis schoutedeni. Here considered a good race from the French Congo and Angola to the Kasai and Northern Rhodesia, distinct from *A. s. nyassae* of Nyasaland and Tanganyika.

Anthus vaalensis saphiroi and *A. v. goodsoni*. Here considered races of *Anthus leucophrys*.

Anthus trivialis sibirica. Here considered a good race breeding in Siberia, distinct from *A. t. trivialis* of Europe in series but not in individual specimens.

Anthus hodgsoni berezowskii. Here considered a synonym of *A. h. hodgsoni*.

Anthus spinoletta meinertzhageni. Here considered a part of a cline between *A. s. petrosus* and *A. s. kleinschmidti*, but closer to the latter, and therefore best listed as a synonym of *A. s. kleinschmidti*.

Anthus spinoletta blakistoni. Here considered a good race breeding in Central Asia, distinct from *A. s. coutelli* from the Caucasus.

Anthus spinoletta harmsi. Here considered as possibly indeterminate but best placed as a synonym of *A. s. japonicus* and not of *A. s. rubescens*.

Anthus spragueii. Here considered possibly as a race of *A. furcatus*.

Anthus sylvanus. The original author and reference should be :—

Heterura sylvana Hodgson, 1845, Proc. Zool. Soc. Lond. p. 33 : Nepal. *not*
Heterura sylvana Blyth, 1845, Journ. Asiat. Soc. Bengal, 14, p. 556 : Nepal.

Hodgson's description was published in August 1845 (see P.Z.S. 1893 : 438). Blyth's paper, in which he quotes Hodgson's description, must have been published after August, since it is in the same part (number 164) of the J.A.S.B. as a paper dated 29th August 1845 (p. 602). This gives priority, as is fitting, to Hodgson's description.

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PLATE 56

SOME ASIATIC PIPITS

Richard's Pipit

FIG. 1. *Anthus novaeseelandiae richardi.*

FIG. 2. *Anthus novaeseelandiae waitei.*

FIG. 3. *Anthus novaeseelandiae malayensis.*

Tawny Pipit

FIG. 4. *Anthus campestris campestris.*

FIG. 5. *Anthus campestris kastschenkoi* (young)

Blyth's Pipit

FIG. 6. *Anthus godlewskii.*

Long-billed Pipit

FIG. 7. *Anthus similis similis.*

FIG. 8. *Anthus similis jerdoni.*

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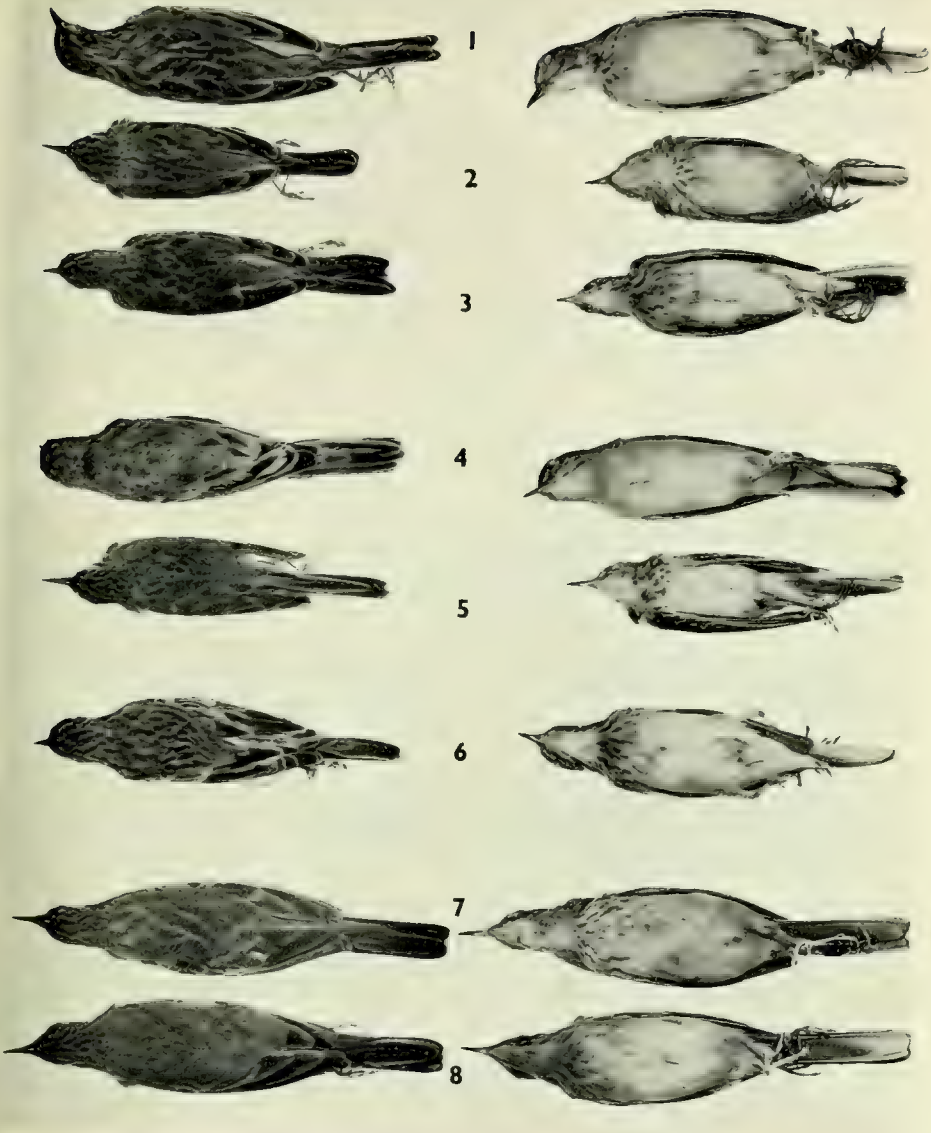
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PLATE 57

SOME AFRICAN PIPITS

Richard's Pipit

FIG. 1 *Anthus novaeseelandiae cinnamomeus* (dark).

FIG. 2 *Anthus novaeseelandiae cinnamomeus* (normal).

FIG. 3 *Anthus novaeseelandiae bocagei.*

FIG. 4. *Anthus novaeseelandiae lwenarum.*

Long-billed Pipit

FIG. 5 *Anthus similis schoutedeni.*

FIG. 6. *Anthus similis nicholsoni.*

FIG. 7. *Anthus similis jebelmarrae.*

Plain-backed Pipits

FIG. 8 *Anthus leucophrys leucophrys.*

FIG. 9. *Anthus vaalensis vaalensis.*

FIG. 10. *Anthus pallidiventris pallidiventris.*

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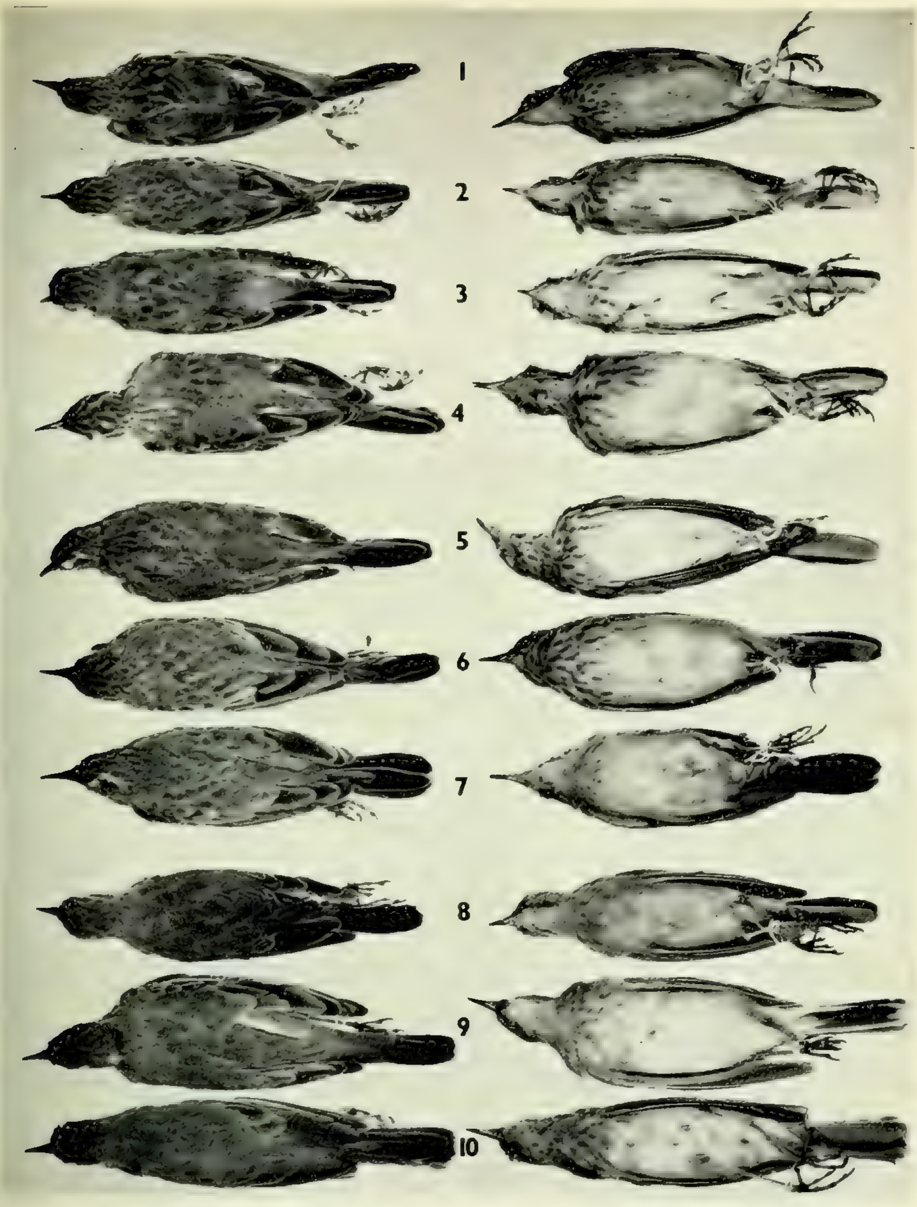
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PLATE 58

SOME PALEARCTIC PIPITS

Meadow Pipit

FIG. 1. *Anthus pratensis pratensis.*

FIG. 2. *Anthus pratensis theresae.*

Tree Pipit

FIG. 3. *Anthus trivialis trivialis.*

FIG. 4. *Anthus trivialis haringtoni.*

Indian Tree Pipit

FIG. 5. *Anthus hodgsoni hodgsoni.*

FIG. 6. *Anthus hodgsoni yunnanensis.*

Hodgson's Pipit

FIG. 7. *Anthus roseatus* (autumn).

FIG. 8. *Anthus roseatus* (spring).

Red-throated Pipit

FIG. 9. *Anthus cervinus* (spring ♂).

FIG. 10. *Anthus cervinus* (autumn ♀).

Pechora Pipit

FIG. 11. *Anthus gustavi gustavi.*

FIG. 12. *Anthus gustavi menzbieri.*

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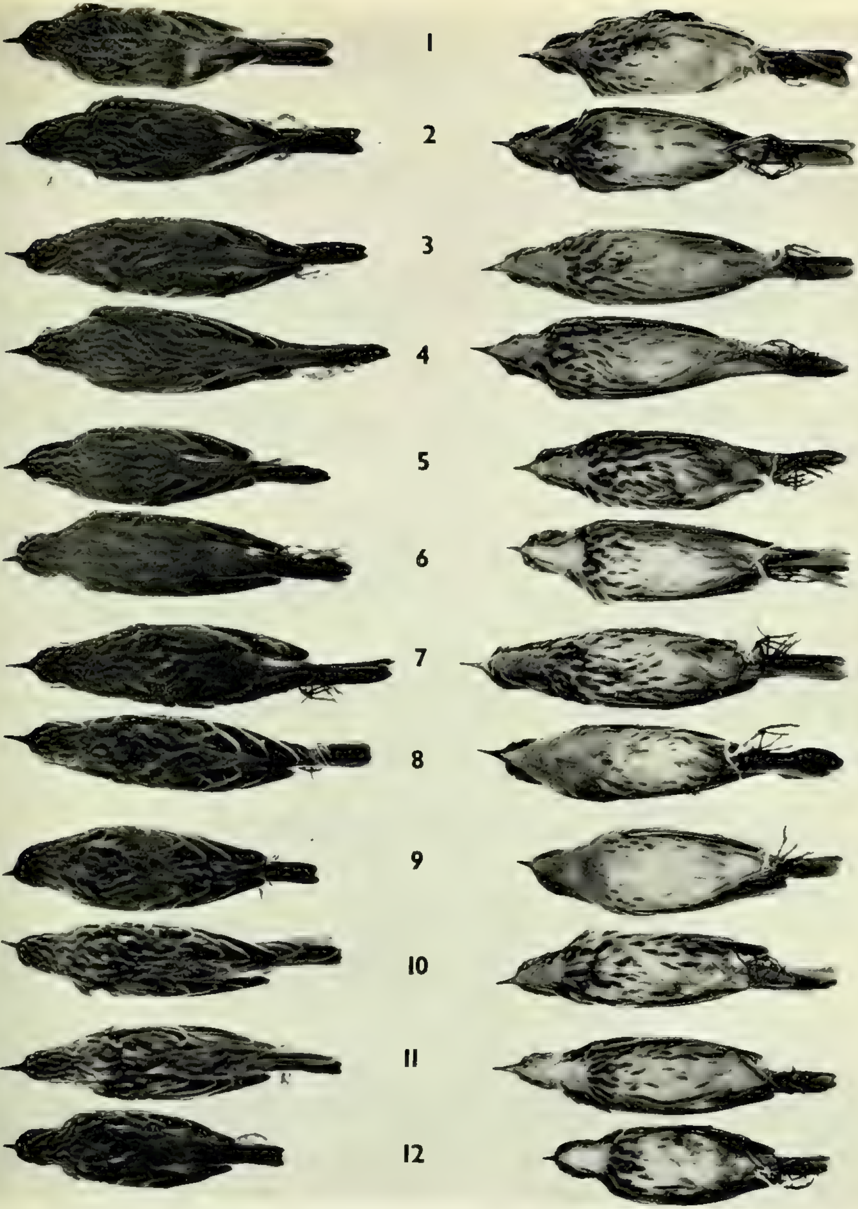
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PLATE 59

SOME ROCK AND WATER PIPITS

Water Pipits

Fig. 1. *Anthus spinoletta spinoletta* (autumn).

Fig. 2. *Anthus spinoletta spinoletta* (spring).

Fig. 3. *Anthus spinoletta blakistoni* (autumn).

Fig. 4. *Anthus spinoletta blakistoni* (spring).

Fig. 5. *Anthus spinoletta japonicus* (autumn).

Fig. 6. *Anthus spinoletta japonicus* (spring).

Rock Pipits

Fig. 7. *Anthus spinoletta petrosus* (autumn).

Fig. 8. *Anthus spinoletta petrosus* (spring).

Fig. 9. *Anthus spinoletta littoralis* (spring).

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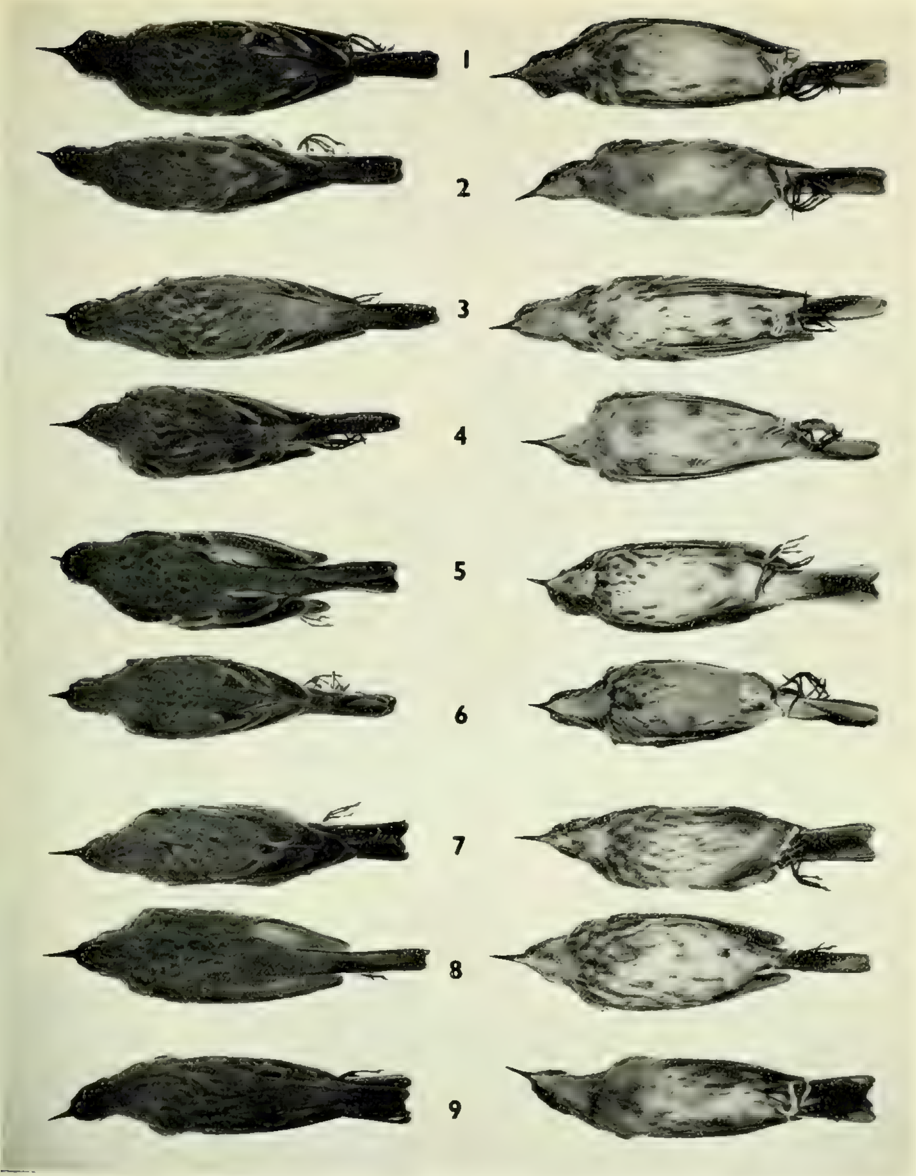
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PLATE 60

Second outermost rectrices, wing tips and hind claws of Richard's Pipit (*A. novaeseelandiae*), the Tawny Pipit (*A. campestris*), Blyth's Pipit (*A. godlewskii*), the Long-tailed Pipit (*A. similis*), and the Plain-backed Pipits (*A. vaalensis*, *A. leucophrys* and *A. pallidiventris*).

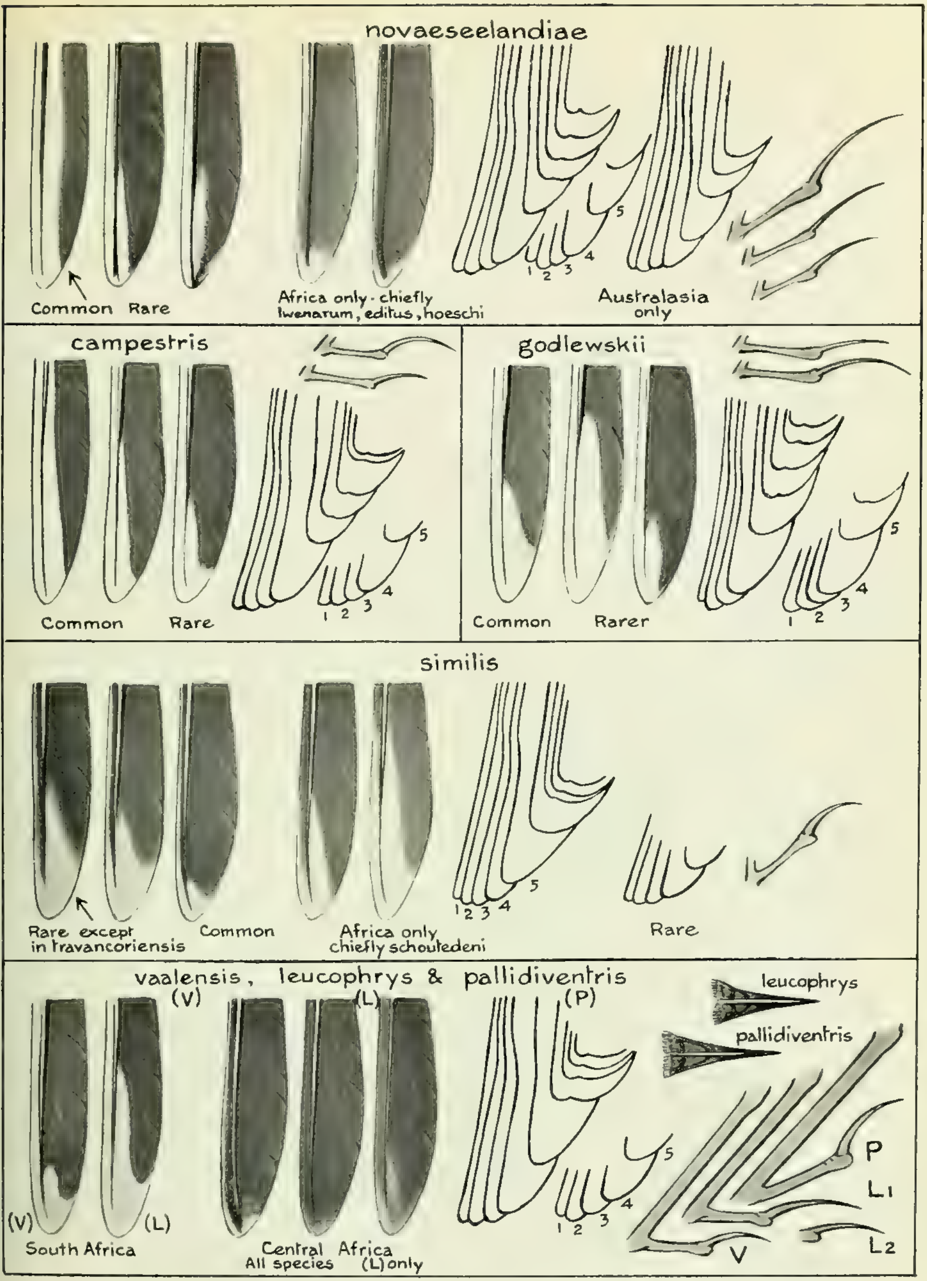
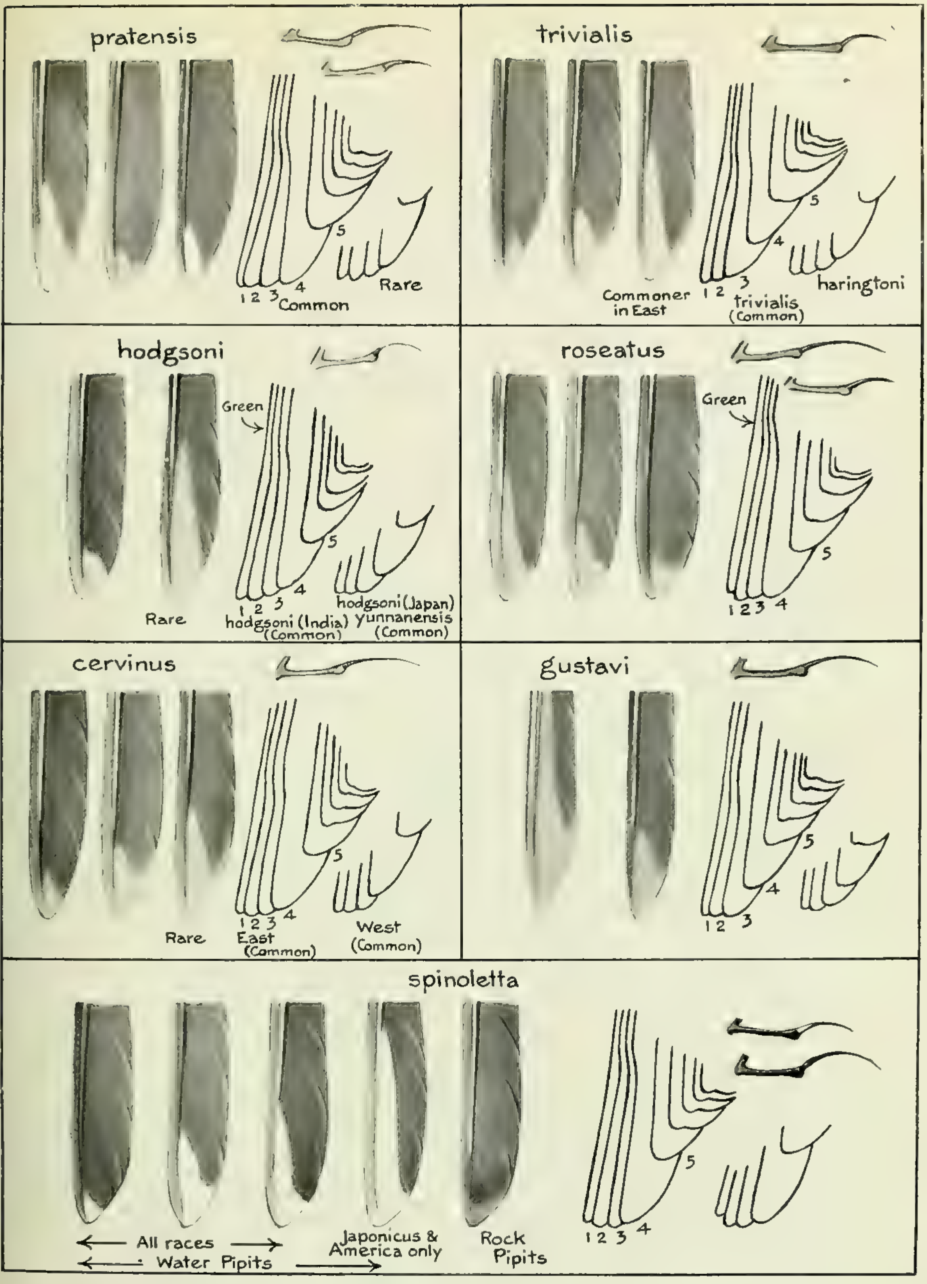

novaeseelandiae
Common
Rare
Africa only - chiefly lwenarum, editus, hoeschi
1 2 3 4 5
Australasia only
campestris
Common
Rare
1 2 3 4 5
godlewskii
Common
Rarer
1 2 3 4 5
similis
Rare except in travancoriensis
Common
Africa only chiefly schoutedeni
1 2 3 4 5
Rare
vaalensis, leucophrys & pallidiventris
(V)
(L)
(P)
leucophrys
pallidiventris
(V)
(L)
South Africa
Central Africa
All species
(L) only
1 2 3 4 5
P
L1
L2
V

PLATE 61

Second outermost rectrices, wing tips and hind claws of the Meadow Pipit (*A. pratensis*), the Tree Pipit (*A. trivialis*), the Indian Tree Pipit (*A. hodgsoni*), Hodgson's Pipit (*A. roseatus*), the Red-throated Pipit (*A. cervinus*), the Pechora Pipit (*A. gustavi*), and the Rock and Water Pipits (*A. spinoletta*)


pratensis
1 2 3 4 5
Common
Rare
trivialis
1 2 3 4 5
Commoner in East
trivialis (Common)
haringtoni
hodgsoni
Green
1 2 3 4 5
Rare
hodgsoni (India) (Common)
hodgsoni (Japan) yunnanensis (Common)
roseatus
Green
1 2 3 4 5
cervinus
1 2 3 4 5
Rare
East (Common)
West (Common)
gustavi
1 2 3 4 5
spinoletta
All races
Water Pipits
Japonicus & America only
Rock Pipits
1 2 3 4 5

[illegible]

FREE-LIVING NEMATODES FROM SOUTH AFRICA

WILLIAM G. INGLIS

AND

THE SPECIES OF *RHABDITIS* (NEMATODA) FOUND IN ROTTING SEAWEED ON BRITISH BEACHES

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PRESENTED

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ZOOLOGY Vol. 7 No. 6
LONDON : 1961

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BY

WILLIAM G. INGLIS

Pp. 291–319; 37 *Text-figures*

AND

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Pp. 320–333; 4 *Text-figures*

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FREE-LIVING NEMATODES FROM SOUTH AFRICA

By WILLIAM G. INGLIS

SYNOPSIS

Five new species of free-living nematodes are described from the mouth of the Greater Kleinemonde River, Cape Province, South Africa. They are named: *Trissonchulus janetae*, *Mesonchium nini*, *Hypodontolaimus angelae*, *Polygastrophora omercooperi* and *Sphaerolaimus anterides*. *Trissonchulus* Cobb, 1920 is accepted as a valid genus with six species: *T. oceanus* Cobb, 1920 (type species); *T. obtusus* (Bresslau and Schuurmans Stekhoven, 1935) comb. nov.; *T. nudus* (Schuurmans Stekhoven, 1943) comb. nov.; *T. reversus* Chitwood, 1951; *T. latus* (Wieser, 1953) comb. nov.; *T. janetae* sp. nov. Wieser's (1954*b*) treatment of *Pepsonema* Cobb, 1920 as a synonym of *Mesonchium* Cobb, 1920, is accepted but his treatment of *Spilophora canadensis* Cobb, 1914, as a synonym of *Hypodontolaimus geophila* (de Man, 1876) is not. *S. canadensis* is considered a *species inquirendum*. *Bolbella cylindricauda* Allgén, 1959 is shown to be a species of *Polygastrophora* and is treated as a synonym of *P. hexabulba* (Filipjev, 1918).

Professor J. Omer-Cooper made a small collection of free-living nematodes at the mouth of the Greater Kleinemonde River in the Bathurst District of Cape Province, Union of South Africa. Fuller details of this locality have been given by Omer-Cooper (1957*a*; 1957*b*) but it may be noted here that the mouth of the river is closed by a sandbar for much of each year and, sometimes, continuously for more than one year. Behind the bar a lagoon is formed the salinity of which " . . . is normally between 23·3 and 34·0 per mille, but it has reached 41·2 per mille during a long drought . . . " (Omer-Cooper, 1957*a*). The nematodes were collected by sieving mud and, as their collection was not the primary object of the survey, the majority of the specimens are large. Nevertheless seven species (and genera) are represented, but two are insufficiently preserved to warrant a full study. They could be identified to genera but are not listed as the literature already contains too many references to genera only. Further the genera are cosmopolitan and frequent in occurrence so that it is not surprising that species referable to them should occur in South Africa and as the species are almost certainly common they will be found again. The remaining five species, all previously unknown, are described here as new, and are all referable to existing genera.

The five species are:

Trissonchulus janetae sp. nov. (p. 294).
Mesonchium nini sp. nov. (pp. 301).
Hypodontolaimus angelae sp. nov. (pp. 305).
Polygastrophora omercooperi sp. nov. (pp. 309).
Sphaerolaimus anterides sp. nov. (pp. 313).

These species, although taken in brackish water, belong to genera which are otherwise known only from wholly marine localities. This does not indicate anything of importance since it is already fairly well established that characteristically marine nematodes can occur in brackish water, such habitats usually having a mixture of marine and fresh-water forms. That all five species are marine forms is not surprising since they were collected by sieving mud and under such circumstances one would expect only the larger forms to be gathered. The number of specimens in the collection and their sizes support this. Since the marine species are generally larger than fresh-water or soil forms their sole presence in the samples from Kleinemonde is a reflection of the collecting method used rather than of the fauna present. No conclusions of a zoo-geographical nature may be drawn since, as the present collection well demonstrates, free-living marine nematodes are insufficiently known on a world basis to make such an exercise either interesting or profitable (see also Chitwood (1951) who makes the same point).

Trissonchulus janetae sp. nov.

Material Studied

60 + ♂; 60 + ♀; 30+ larvae. B.M. (N H.), Reg. Nos. 1960.123–272. 1 ♂ selected as Holotype, 1960.123.

Proportions and Measurements (*mm.*)

	a	*b*	*c*	V	Body length
♂♂	39·9	4·9	32·3	—	3·55
	39·6	4·9	28·7	—	3·84
	39·2	5·2	31·0	—	3·88
	43·4	5·7	31·1	—	4·08
	47·1	5·9	34·2	—	4·10
	48·2	5·8	31·7	—	4·53
	48·7	6·0	32·0	—	4·58
♀♀	39·7	5·3	34·2	54·4	4·10
	39·8	5·4	31·5	56·1	4·10
	36·6	5·3	31·5	55·7	4·13
	41·7	5·1	32·6	57·0	4·30
	45·0	5·7	31·6	56·0	4·68
	41·0	5·8	30·7	53·8	4·72
	45·3	6·1	29·3	55·2	4·98
Larvae	36·2	4·0	23·6	—	2·10
	43·3	4·6	28·6	—	3·38
	42·7	5·3	29·1	—	3·54

Males (all measurements in the order of the body lengths) : Oesophagus length : 0·72 ; 0·78 ; 0·74 ; 0·71 ; 0·69 ; 0·78 ; 0·76. Pharyngeal-rod length : 0·092 ; 0·094 ; 0·097 ; 0·087 ; 0·098 ; 0·089 ; 0·087. Head diameter (level at anterior edge of amphid) : 0·033 ; 0·034 ; 0·032 ; 0·034 ; 0·032 ; 0·033 ; 0·036. Amphid width (head diameter/amphid width) : 0·090 (3·7) ; 0·090 (3·8) ; 0·010 (3·2) ; 0·010 (3·4) ;

0·009 (3·6) ; 0·010 (3·3) ; 0·009 (4·0). Amphid length : 0·010 ; 0·010 ; 0·010 ; 0·009 ; 0·010 ; 0·010 ; 0·011. Amphid from anterior end (=depth of cephalic cap) : 0·021 ; 0·019 ; 0·018 ; 0·019 ; 0·012 (teeth strongly retracted) ; 0·020 ; 0·022. Excretory pore from anterior end : 0·024 ; ... ; 0·023 ; ... ; 0·021 ; ... ; 0·029. Nerve ring from anterior end : 0·25 ; 0·23 ; 0·26 ; 0·28 ; 0·23 ; 0·31 ; 0·38. Tail length (tail length/anal diameter) : 0·110 (1·6) ; 0·133 (1·9) ; 0·125 (1·7) ; 0·131 (1·7) ; 0·120 (2·0) ; 0·143 (2·0) ; 0·143 (1·9). Spicule length : 0·093 ; 0·096 ; 0·097 ; 0·104 ; 0·097 ; 0·098 ; 0·099. Gubernaculum length : 0·047 ; 0·055 ; 0·055 ; 0·062 ; 0·056 ; 0·058 ; 0·060.

Females : Oesophagus length : 0·78 ; 0·76 ; 0·78 ; 0·84 ; 0·82 ; 0·81 ; 0·82. Pharyngeal rod length : 0·091 ; 0·082 ; 0·097 ; 0·086 ; 0·087 ; 0·085 ; 0·097. Head diameter (level at anterior edge of amphid) : 0·031 ; 0·034 ; 0·030 ; 0·036 ; 0·034 ; 0·035 ; 0·034. Amphid width (head diameter/amphid width) : 0·009 (3·4) ; 0·010 (3·4) ; 0·009 (2·2) ; ... (...) ; 0·010 (3·4) ; 0·009 (3·9) ; 0·010 (2·4). Amphid length : 0·010 ; 0·011 ; 0·009 ; ... ; 0·010 ; 0·009 ; 0·011. Amphid from anterior end (= depth of cephalic cap) : 0·019 ; 0·015 ; 0·018 ; 0·019 ; 0·022 ; 0·023 ; 0·017. Nerve ring from anterior end : 0·25 ; 0·36 ; ... ; ... ; 0·27 ; 0·29 ; 0·32. Excretory pore from anterior end : 0·020 ; ... ; ... ; ... ; 0·021 ; 0·022 ; 0·022. Tail length (tail length/anal diameter) : 0·120 (1·7) ; 0·130 (1·9) ; 0·131 (1·9) ; 0·132 (1·8) ; 0·148 (2·1) ; 0·154 (1·9) ; 0·170 (2·2). Vulva from anterior end : 2·2 ; 2·3 ; 2·3 ; 2·5 ; 2·6 ; 2·5 ; 2·8.

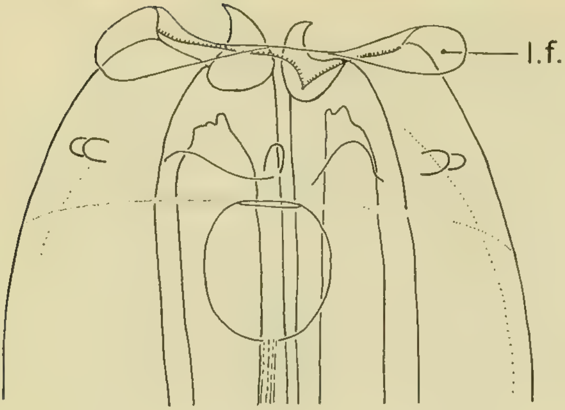
Larvae : Oesophagus length : 0·52 ; 0·74 ; 0·67. Pharyngeal-rod length : 0·060 ; 0·074 ; 0·081. Head diameter (level at anterior edge of amphid) ; 0·033 ; 0·031 ; 0·044. Amphid width (head diameter/amphid width) ; 0·077 (4·7) ; 0·070 (4·4) ; 0·080 (5·6). Amphid length : 0·009 ; 0·009 ; 0·009. Amphid from anterior end (= depth of cephalic cap) : 0·014 ; 0·016 ; 0·017. Nerve ring from anterior end : 0·19 ; 0·25 ; 0·27. Excretory pore from anterior end : ... ; 0·024 ; 0·027. Tail length (tail length/anal diameter) : 0·089 (2·0) ; 0·118 (2·1) : 0·122 (2·0). Secondary teeth from anterior end : 0·019 ; 0·023 ; 0·016.

Cuticle

The cuticle is smooth without markings.

Head and Oesophagus

The head bears an inner circle of six small, sessile papillae and an outer circle of ten prominent papillae of which four are markedly larger than the others (Text-figs. 2 and 4). Laterally, between the lateral papillae of the inner and outer circles, is another structure, pore-like in appearance, which appears to correspond with the cephalic slits found in the Enoploidea. Such slits do not appear to have been reported from this genus before. The mouth opening is closed by three rather thin lip-flaps. The anterior end of the oesophagus bears a pair of smallish, wholly cuticular teeth dorsally and a single, larger, comparable tooth on each ventro-lateral sector (Text-figs. 1, 3 and 5). The anterior edges of the lumen of the oesophagus bear a row of small denticles exactly the same in appearance and distribution as the denticles



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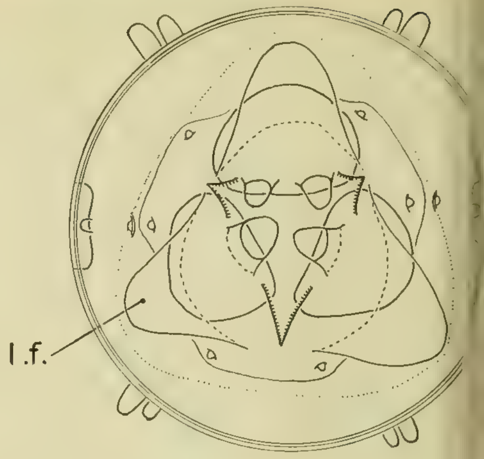

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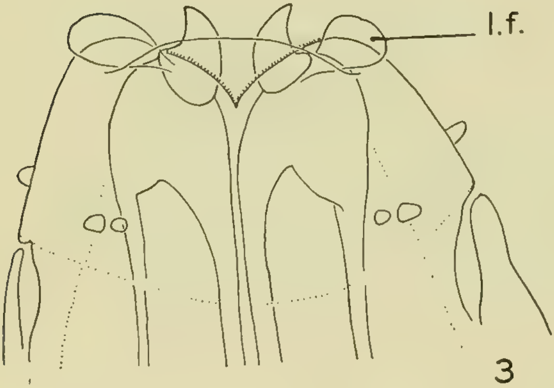

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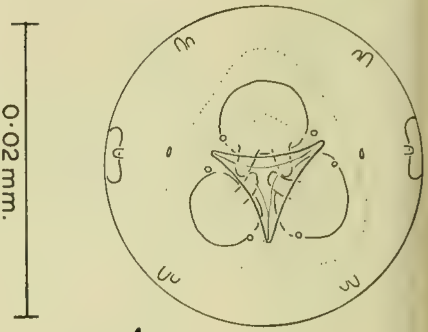

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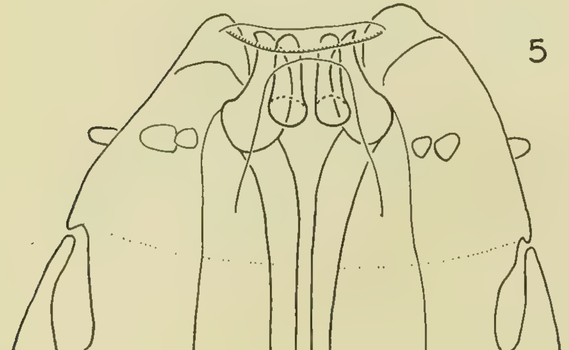

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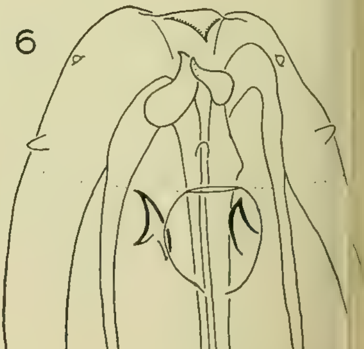


6

found within the mouth of species of the genus *Enoplus*. When the mouth is open the teeth are pulled anteriorly so that they project through the mouth opening and the lip-lobes are folded back over the head (Text-figs. 1, 2 and 3, l.f.). When the mouth is closed the two ventro-lateral teeth come together to lie between the two-dorsal teeth (Text-fig. 4). The amphids are pouch-like and their anterior edges lie exactly on the posterior edge of the cephalic cap.

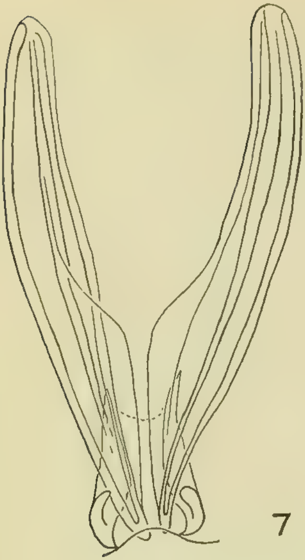
The oesophagus expands evenly along its length so that there is no definite posterior swelling or bulb. Anteriorly it is modified as a distinct pharynx lined by very distinct cuticular rods, here called pharyngeal-rods. The posterior ends of the pharyngeal-rods are very distinct and blunt (Text fig. 8). The musculature surrounding the rods is directed antero-radially rather than wholly radially as it is in the remainder of the oesophagus. The pharyngeal region is not markedly stouter than the rest of the oesophagus in most specimens but it does swell out in some. It is probable that the swollen condition is the more natural since the specimens appear to have been stretched during fixation. The extreme anterior end of the pharynx, from about the level of the amphids, is capped by cuticle (= pharyngeal capsule) and is fused to the body-wall dorsally and ventro-laterally (i.e. at three points). A definite, although indistinct, cephalic capsule is present which coincides posteriorly with the anterior limits of the amphids but I have been unable to determine the anterior limits i.e. there is no definite stomodaeal ring (terminology of Wieser, 1954*a*). Because of this fusion of the pharynx with the body cuticle the pharynx is triangular in cross section (Text-figs. 2 and 4).

In the larvae there is, in all the specimens studied (about twenty), a second set of teeth lying about the level of the amphids (Text fig. 6). These teeth are identical in structure and number with those found anteriorly. The dorsal are about 0·005 mm. long while the ventro-lateral are about 0·008 mm. long. In one specimen which appeared to be otherwise fully adult, with fully developed spicules, gubernaculum and reproductive system (body length 4·08 mm.) such a second set of teeth was present, 0·021 mm. from the anterior end. This I have interpreted as an abnormality and have included the measurements of the specimen under the males.

Tail

The tail is relatively very short ($c = 28{\cdot}7 — 34{\cdot}2$ in the adults), and ends bluntly posteriorly, particularly in the adults as there is a tendency for it to be more rounded in the larvae and smaller adults. The spinerette opens dorsally (Text-figs. 11 and 13)

Figs. 1–6. *Trissonchulus janetae* sp. nov., the structure of the head. Fig. 1. Lateral view of adult head with the dorsal side towards the right. The mouth is open and the lip-flaps are folded back over the anterior end of the body. Fig. 2. *En face* view of adult head with mouth open and lip-flaps folded back. Fig. 3. Head, as Fig. 1, from the ventral aspect. Fig. 4. *En face* view of larval head. The mouth is closed, note the relationships between the dorsal and ventro-lateral teeth. Fig. 5. Head, as Figs. 1 and 3, from the dorsal aspect. Fig. 6. Larval head from the lateral aspect with dorsal side to the right. Note secondary teeth. (All figures to the same scale.) (l.f. = lip-flaps.)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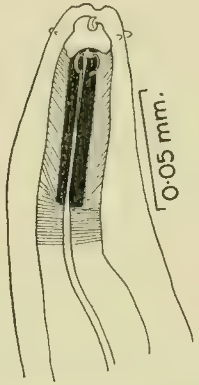

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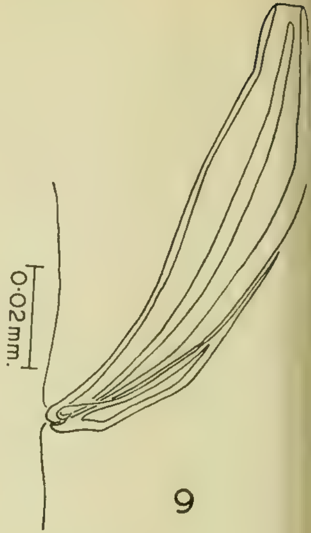

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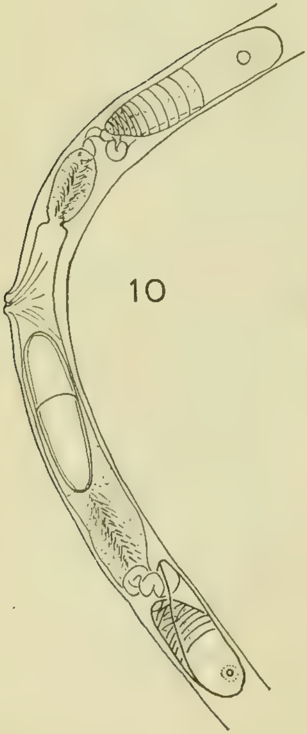
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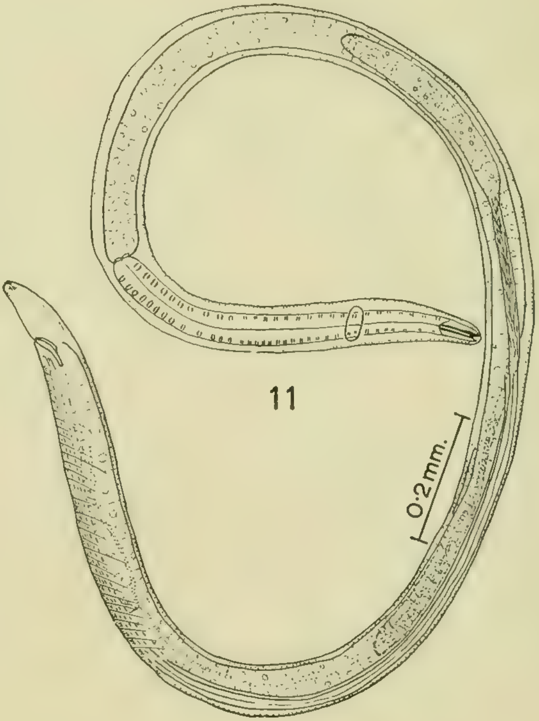

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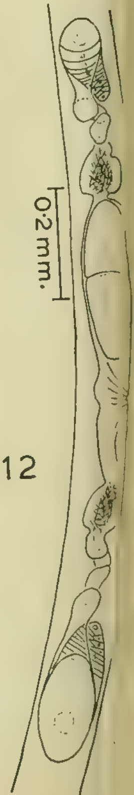

12

and there are several sessile papillae scattered over the surface in both males and females, but there are no setae.

Male

The spicules are short, equal in length, stout and complicated, with blunt posterior tips. They show a distinct central bar of thickening from which alae appear to arise when they are viewed from the ventral aspect (Text-fig. 7). The gubernaculum is relatively short and is indistinct anteriorly. Posteriorly it is thick and is developed into two claw-like structures which enfold the spicules and also appear to support the posterior edge of the cloacal opening (Text-figs. 7 and 9). There are no special caudal papillae or pre-cloacal supplements but there is a series of muscle bands running from the dorso-lateral part of the body ventrally and posteriorly. These bands occur over a region equal in length to about one third of the length of the body.

There are two opposed testes of which the anterior is slightly longer than the posterior. They lead into a pair of long narrow seminal vesicles from the junction of which a very thick-walled vas deferens runs posteriorly to the cloaca (Text-fig. 11). The seminal vesicles contain flagellate sperm (see Chitwood & Chitwood, 1951, p. 156 and fig. 125M).

Female

The reproductive apparatus, which consists of two opposed uteri with associated reflexed ovaries, is relatively short in proportion to the length of the body. Thus, from four specimens the following lengths, in mm., of the entire length of the reproductive tract were obtained: length of reproductive tract: body length (body length/length reproductive tract): 1·2 : 4·7 (3·9); 1·8 : 4·7 (2·6); 1·2 : 4·1 (3·4); 1·4 : 4·3 (3·1). The ovaries lead into relatively long narrow oviducts which are modified, just before they join the uteri, as seminal receptacles which generally contain sperm. The eggs are very large, 0·29 mm. × 0·087 mm.; 0·22 mm. × 0·094 mm.; 0·26 mm. × 0·093 mm., and although two eggs have been seen in some specimens there is generally only one present. It appears that the ovaries generally produce an egg alternately since it has been noted that the last cell in the ovarian part of the reproductive tract is generally much larger in the ovary opposite to that in which the egg is present in the uterus (Text-figs. 10 and 12). The eggs themselves appear to have a line round them about the mid-point of their lengths although this has not been seen in all the specimens. Its status is not clear since in all cases where such a line was present only one nucleus could be found so that it does not appear to represent the first division of the egg but may rather represent a modification of the egg shell or simply be due to fixation.

FIGS. 7–12. *Trissonchulus janetae* sp. nov. Fig. 7. Ventral view of spicules and gubernaculum. Fig. 8. Lateral view of anterior end of body showing structure of pharyngeal part of the oesophagus. Fig. 9. As Fig. 7, from the lateral aspect. Fig. 10. Female reproductive apparatus. Note flagellate sperm in oviducts. Fig. 11. Whole male. Fig. 12. Female reproductive apparatus. (Figs. 7 and 9; 10 and 12 to the same scale.)

Discussion

Schuurmans Stekhoven (1950) argues that *Trissonchulus* Cobb, 1920 should not be considered distinct from *Dolicholaimus* de Man, 1888, and Wieser (1953*b*) accepts this, since he could not see any difference between the two genera except the shape of the tail, which is long and narrow in *Dolicholaimus* and short, wide and blunt in *Trissonchulus*. Gerlach (1954) apparently accepts this since he does not include *Trissonchulus* in his key to the marine genera of the Ironidae. However, there does appear to be a further difference between the species with long tails and those with short. There is only a single dorsal tooth in those with long tails while some, at least, of the short tailed species are known to have two teeth dorsally. Five short tailed species have been described : *T. oceanus* Cobb, 1920 (type species of the genus) which was described as having three teeth ; *D. obtusa* Bresslau and Schuurmans Stekhoven, 1935 (in Schuurmans Stekhoven, 1935) described as having two teeth dorsally and two ventrally (Chitwood (in Chitwood & Chitwood, 1950) states that this species has three double equal odontia but gives no figure and has probably misunderstood the original description) ; *D. nudus* Schuurmans Stekhoven, 1943 has been described as having " three spears with biuncinate apex " (Schuurmans Stekhoven, 1950) but the figures do not support this interpretation and suggest that two teeth are present on the dorsal side of the head only ; *D. latus* Wieser, 1953*b*, in which the written description is very short, suffers because of Wieser's declared policy that " No organs will be described morphologically in the text if their structure can be inferred from the figure." (Wieser, 1953*b*, p. 8). Unfortunately Wieser only mentions three teeth and gives a figure which is on such a small scale that it is impossible to obtain any information about the structure or arrangement of the teeth. Finally Chitwood (1951) described *T. reversus* from a single juvenile, the teeth are not mentioned and the figure of the head does not allow the number of teeth to be established (see also Chitwood and Timm (1954) where Chitwood's 1951 figures are reproduced). In spite of this uncertainty about the number and arrangement of the teeth in the various short tailed species I think that the genus *Trissonchulus* should be recognized for the species with short, stout, blunt tails since I suspect that adequate morphological studies will demonstrate the presence of two dorsal teeth in them all. Even if this should not be so the difference between the tail shapes in the two groups certainly warrants generic separation. The genus *Trissonchulus* may be diagnosed thus :

Trissonchulus Cobb, 1920

Ironidae : sense organs of head papilliform ; mouth opening bounded by three lip-flaps ; two small teeth, identical in structure present on anterior end of dorsal sector of pharynx (?) ; one large tooth on each ventro-lateral sector (?) ; tail short, stout and blunt.

Type species : *Trissonchulus oceanus* Cobb, 1920.

Other Species : *T. obtusus* (Bresslau and Schuurmans Stekhoven in Schuurmans Stekhoven, 1935) comb. nov.; *T. nudus* (Schuurmans Stekhoven, 1943) comb. nov.; *T. reversus* Chitwood, 1951 ; *T. latus* (Wieser, 1953) comb. nov.; *T. janetae* sp. nov.

T. janetae is easily distinguished from all the other species of the genus *Trisson-*

chulus, except *T. reversus*; by the dorsal opening of the spinerette. Chitwood reports the same condition in *T. reversus* together with a figure of the tail and a figure of the anterior end of the body. The written description, which was based on one juvenile specimen, is otherwise restricted to the body length (1·16 mm.), the ratios *a* (29), *b* (3·2), *c* (16) and the length of the stoma (0·040 mm.) (= length of pharyngeal rods ?). Although this description leaves much to be desired the value for "*a*" is much lower than the values obtained for *T. janetae* larvae even when the differences between the lengths of the bodies is considered. The differences between the "*b*" values are probably not significant but "*c*" does appear to be sufficiently low to be significant. Nevertheless it is impossible to be sure of the relationship between *T. janetae* and *T. reversus* and I have considered it better to name the specimens from South Africa as new until the developmental stages of both nominal species are known.

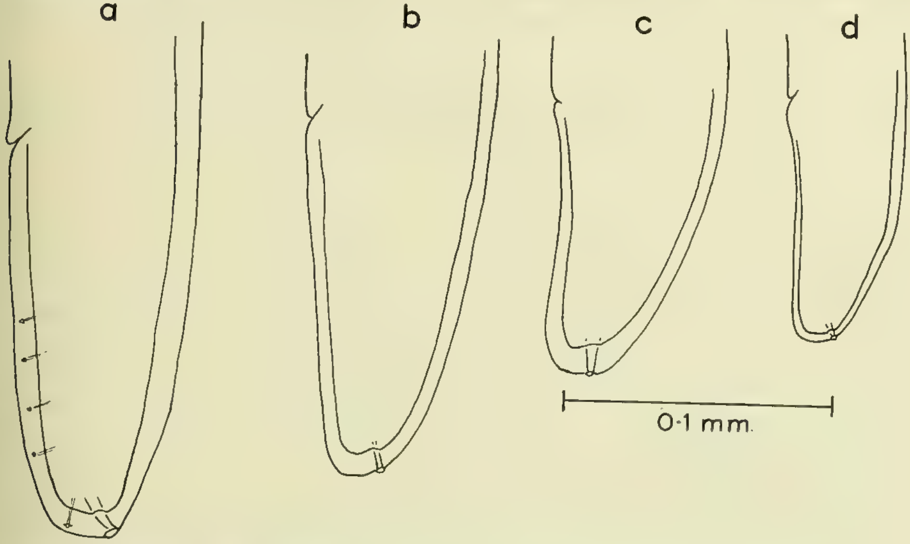

FIG. 13. Outlines of the tails of various specimens: *a* and *b*, adult females, *c*, adult male and *d*, larva. (All to same scale.)

Mesonchium nini sp. nov.

Material Studied

1 ♂, 2 ♀ B.M. (N.H.), Reg. Nos. 1960.297–299. ♂ selected as Holotype. The specimens are in a rather poor condition.

Proportions and Measurements (mm.).

	a	*b*	*c*	V	Body length
♂	36·4	9·5	13·9	—	1·93
♀♀	34·2	8·5	11·1	43·3	1·78
	45·2	8·2	11·3	48·6	2·08

Male (Holotype) : Oesophagus length : 0·204. Head diameter : 0·010. Pharynx depth : 0·021. Distance from anterior end to anterior edge of amphids : 0·006. Amphid diameter : 0·007. Diameter of head at amphid : 0·013. Diameter of amphid as percentage of head diameter : 53·8. Nerve ring from anterior end : 0·097. Excretory pore not seen. Tail length (tail length/anal diameter) : 0·139 (3·6). Spicule length : 0·082. Gubernaculum length (= length posterior apophosis) : 0·036.

Females (in order of body lengths) : Oesophagus length : 0·210 ; 0·253. Head diameter : 0·012 ; 0·010. Pharynx depth : 0·020 ; 0·023. Distance from anterior end to anterior edge of amphids : 0·004 ; 0·006. Amphid diameter : 0·008 ; 0·008. Diameter of head at amphid : 0·015 ; 0·016. Diameter of amphid as percentage of head diameter : 53·3 ; 50·0. Nerve ring from anterior end : 0·082 ; 0·089. Excretory pore not seen. Tail length (tail length/anal diameter) : 0·160 (4·3) ; 0·184 (4·7). Vulva from anterior end : 0·77 ; 1·01.

Cuticle

The surface of the body, dorsally and ventrally is marked by fine striations while the cuticle is differentiated laterally by a series of dots. This differentiation, from about the level of the posterior end of the oesophagus to just anterior to the cloacal opening or anus takes the form of two files* of large, rectangular, spectacularly distinct dots which lie in a strip of otherwise undifferentiated cuticle. There is, therefore, a clear space on each side of the files of dots. This clear strip is roughly twice as wide as the distance between the two files of dots so that the zones flanking the files of dots are roughly half the distance between two files in width. The clear space is bordered on both sides by a region, roughly the same width as the clear strip, in which the cuticle is differentiated by small dots of which one row corresponds with each set of large rectangular dots and one row corresponds with the space between each contiguous set of rectangles (Text-fig. 16). The clear space, which is about 0·007 mm. in width in all the specimens, is delimited from the outer small dots by a distinct line which may be an artifact. Anteriorly and posteriorly there are four files of smaller, squarer dots which lie equidistant from each other transversely, are not set off from the remainder of the cuticular markings by a clear space and are flanked by rather elongate cuticular markings arranged in rows which correspond one to each row of the larger lateral markings. The smaller elongate markings continue round the body so that there are no dorsal and ventral zones in which the cuticle is undifferentiated as there are on the body opposite the two files of large markings. Four files are present anteriorly from just posterior to the amphids to about the posterior end of the oesophagus (Text-fig. 18) and posteriorly from about the anus, or cloaca, almost to the tip of the tail. The transition from the four files to the two files is remarkably regular. Anteriorly the four files begin to approach each other in pairs until the individual elements of the four files fuse to produce the two files of larger rectangles characteristic of the middle region of the body (Text-fig. 16). At the same time the nature of the markings external to the files changes from the elongate form, in which each row corresponds with each set of lateral markings, to the punctate form in which there is one row corresponding to each row of larger rectangles and one row between each row of rectangles. The lines bordering the undifferentiated strip in which the two files lie correspond exactly with the outer limits of the outer files of the four file zone. This explains why the large rectangles are separated from each other, radially, by a distance twice as great as the width of the clear zones which flank them. Because the four files have fused with perfect symmetry the two files lie exactly midway between the files of each pair in the four file zone (Text-fig. 16). The interpretation of the large dots as representing two fused small dots is confirmed by the presence among the former of many in which only one half is well developed or in which one half has completely failed to develop. The rate at which the four rows approach each other in pairs may vary so that in some cases there are three rows for a short distance. Posteriorly the same change occurs, except that it is reversed, the two files dividing into four as one passes posteriorly.

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* *Files* refers to the arrangement of the dots in lines running antero-posteriorly and *Rows* refers to lines of dots running transversely on the body.

There are two files of relatively long setae running down each side of the body, one file on each side of the lateral differentiation.

Head and Oesophagus

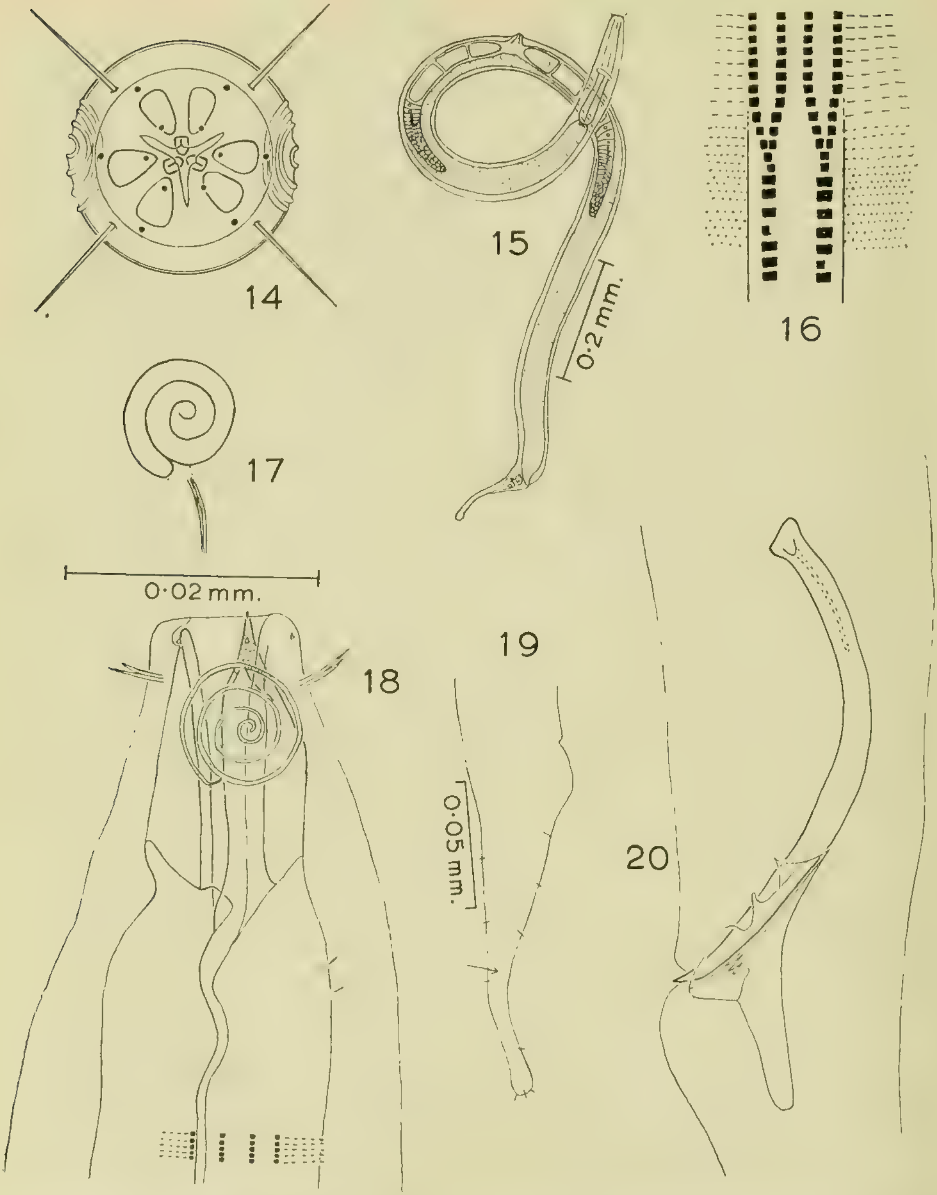
The amphids are spiral and lie relatively far posterior to the anterior end of the body. Both on one female have three and three quarter spirals (Text-fig. 18), both on the male have three and a quarter (Text-fig. 17) while on the second female the left amphid has three and three quarter spirals and the right has three and a quarter. It should be noted that the difference is restricted to the central part of the spiral. The amphidial spiral, which is an open groove, leads into a covered pouch from which the amphidial nerve leaves, so that the innervation of the amphid is posterior.

The mouth opening is bounded by three lip-flaps which are slightly incised centrally so that they are partly bi-lobed (Text-fig. 14). There are two circles of six small sessile papillae and more posteriorly there is a set of four long setae, 0·007–0·008 mm. in length.

The oesophagus is roughly the same width along its whole length except for a slight even swelling at the posterior end (Text-fig. 15). Anteriorly there are three teeth of which the two ventro-lateral are stouter than the dorsal and project further anteriorly (? artifact) (Text-fig. 18). The thickened cuticle which forms these teeth is continued posteriorly for about 0·020 mm. (see above, pharynx depth) as a lining to the anterior end of the oesophagus.

Male

The spicules are slightly curved, simple, identical without alae or other elaborations and terminate posteriorly in sharp points. The gubernaculum has a distinct posterior apophosis and appears to curve round the spicules proximally. The outline of the part of the gubernaculum which enfolds the spicules is irregular (see Text-fig. 20) and while I am sure that the large mass at the cloacal opening end of the gubernaculum is accurate the presence of the other two protuberances is less certain. There are no pre-cloacal supplements and there do not appear to be any special caudal setae. This is however, most uncertain since many of the setae on the body of the



Figs. 14–20. *Mesonchium nini* sp. nov. Fig. 14. *En face* view of head. Fig. 15. Whole body of female. Fig. 16. Lateral differentiation of body about level of posterior end of oesophagus (semi-diagrammatic). Fig. 17. One form of amphid. Fig. 18. Lateral view of head, dorsal side to the right, showing another variation of the amphid. Fig. 19. Lateral view of female tail, arrow indicates point at which lateral differentiation stops. Fig. 20. Structure of the spicules and gubernaculum from the lateral aspect. (Figs. 14, 17, 18 and 20 to the same scale.)

male specimen appear to have been broken off. Anterior to the cloacal opening are about 25–26 oblique, dorso-ventral muscle strands.

Female

The female tail is identical in outline with that of the male (Text-fig. 19). There are two opposed uteri (Text-fig. 15) and the ovaries are not reflexed. The eggs are 0·069 × 0·032 mm. and there are three in each uterus.

Discussion

This species appears to be very similar to *Mesonchium poriferum* Cobb, 1920, the type species of *Mesonchium*, particularly in the structure of the head, the form of the amphids, the structure of the spicules and gubernaculum and the type of lateral differentiation. In *M. poriferum* Cobb (1920) reports the presence of two rows of lateral gland pores lying outside the lateral differentiation which takes the form of three rows of round cuticular elements in the female and two in the male. The so called lateral gland pores may, in fact, have been the bases of lateral rows of setae which had become broken. Wieser (1954*b*) treats *Pepsonema* Cobb, 1920 as a synonym of *Mesonchium* which appears reasonable. The great similarity between the descriptions of *M. poriferum* and *P. pellucidum* is also clear from the characters by which Chitwood (1951) attempted to separate the two species in his key, *M. poriferum* : Ovaries reflexed ; *P. pellucidum* : ovaries outstretched, in spite of Cobb's statement that in the latter species " The ovaries may be reflexed for a short distance near their blind ends." while in the former " An unusual feature is that the ovaries are reflexed only near their blind ends." *P. pellucidum* appears to differ from *M. poriferum* mainly in the form of the lateral differentiation of the cuticle which is described as " . . . of medium thickness. Anteriorly the number of the longitudinal rows of " beads " appears to be fewer than near the tail, where there are sometimes six or possibly eight rows."

Mesonchium nini can, therefore, be distinguished by the form of the lateral differentiation and possibly by other characters but the descriptions of Cobb's species are insufficient to allow this to be established.

Hypodontolaimus angelae sp. nov.

Material Studied

4 ♂ (one badly damaged, no head), 2 ♀. B.M. (N.H.), Reg. Nos. 1960, 304–309. 1 ♂, 1960, 304 selected as Holotype.

Proportions and Measurements (*mm.*)

	a	*b*	*c*	V	Body length
♂♂	22·6	7·9	9·1	—	1·04
	25·8	7·3	8·2	—	0·98
	22·3	6.3	9·9	—	1·07
♀♀	24·7	7·1	8·1	43·6	1·01 (? 4th larva)
	25·9	8·1	9·2	45·4	1·19

Males (measurements in same order as above): Oesophagus length: 0·132; 0·134; 0·170. Head diameter: 0·014; 0·013; 0·014. Oesophageal bulb, length: 0·031; 0·031; 0·039. Oesophageal bulb, breadth: 0·024; 0·024; 0·023. Nerve ring from anterior end: 0·079; 0·082; . . . Excretory pore: not seen. Tail length (tail length/anal diameter): 0·114 (3·9); 0·120 (3·9); 0·108 (3·2). Spicule length, across chord: 0·038; 0·037; 0·036. Gubernaculum length: 0·030; 0·027; 0·028.

Females: Oesophagus length: 0·142; 0·147. Head diameter: 0·014; 0·014. Oesophageal bulb, length: 0·033; 0·041. Oesophageal bulb, breadth: 0·023; 0·026. Nerve ring from anterior end: 0·079; 0·076. Excretory pore: not seen. Tail length (tail length/anal diameter): 0·124 (4·7); 0·129 (4·6). Vulva from anterior end: 0·44; 0·54.

Cuticle

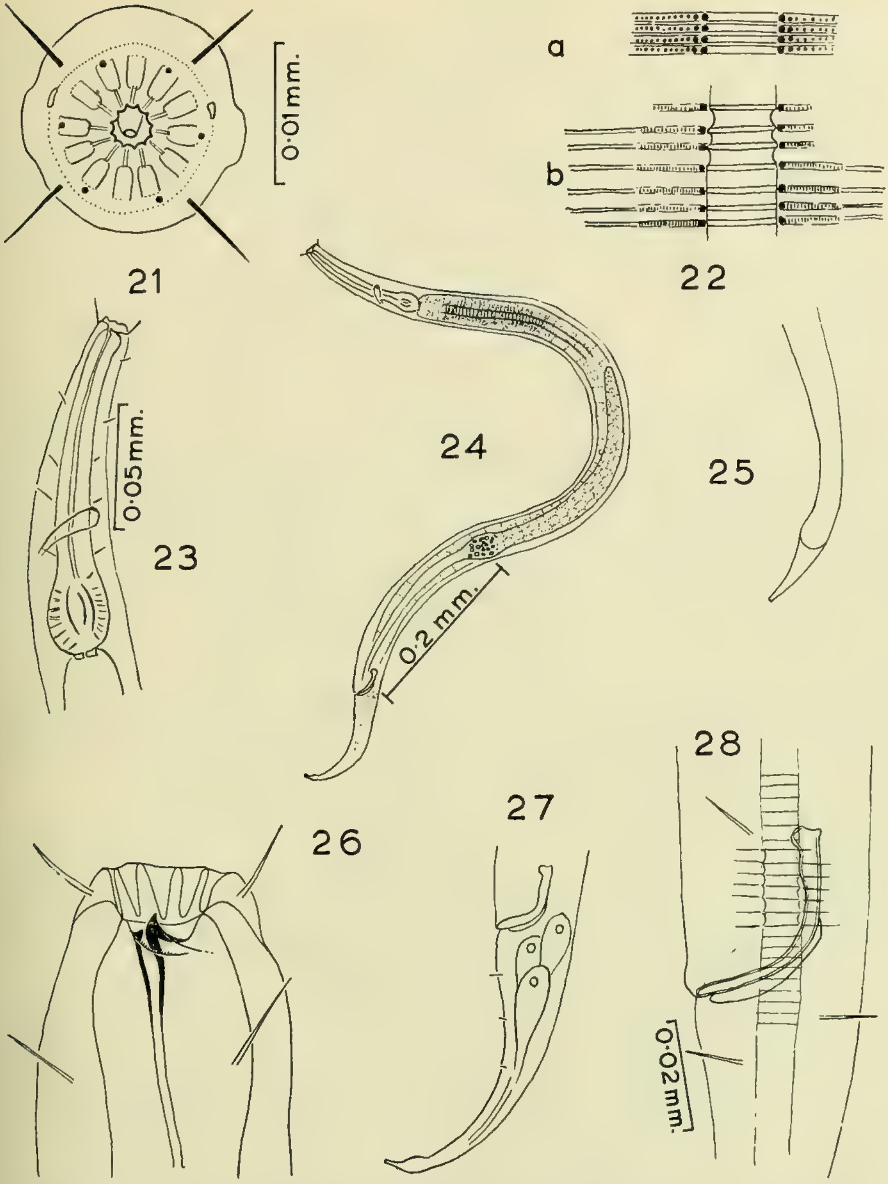
The lateral differentiation starts relatively close to the head and between the head and this point the body is marked by a few rows of circular punctations. Passing posteriorly the cuticle becomes laterally differentiated, with lateral bars which are flanked by large circular dots, one on each side. The remainder of the body is covered by rows of smaller dots (Text-fig. 22, *a*). The main dots become gradually smaller posteriorly while those outside them become narrower and elongate in an antero-posterior direction. From about the level of the posterior end of the oesophagus to just anterior to the level of the anus or cloacal opening the punctations are restricted to a strip on either side of the lateral bars, each strip being roughly the same width as the barred strip (Text-fig. 22, *b*) which varies from 0·003–0·004 mm. just posterior to the head; to 0·004–0·006 mm. about the middle of the body length and becomes narrower again about the level of the anus or cloacal opening where it is 0·003–0·004 mm. in width. The lateral fields are distinctly raised above the remainder of the body surface (Text fig. 21).

There are two files of setae down each side of the body of which the setae are much closer together anteriorly, where they are 0·007–0·008 mm. in length (that is they are longer than the cephalic setae which are 0·006 mm. long), than they are more posteriorly.

Head and Oesophagus

The head is somewhat contracted in all the specimens and, perhaps because of this, an inner circle of papillae has not been seen. One circle of six small, sessile papillae has been seen and there are four long cephalic setae dorso- and ventro-lateral in position (Text-fig. 21). The amphids are latero-subdorsal in position but they are difficult to see and their shape is not clear. The mouth opening is surrounded by the usual twelve ribs which are in two parts, a thick posterior part and an anterior thin part.

The oesophagus has a distinct posterior bulb (Text-fig. 23) and is slightly swollen anteriorly, particularly on the dorsal side, by the muscles which supply the oeso-



FIGS. 21–28. *Hypodontolaimus angelae* sp. nov. Fig. 21. *En face* view of head Fig. 22. Detail of lateral differentiation. *a*, Anterior end of body. *b*. Middle part of body (semi-diagrammatic). Fig. 23. Lateral view of oesophagus. Fig. 24. Whole male, note single gonad. Fig. 25. Detail of extreme tip of tail showing shape of spinerette. Fig. 26. Lateral view of head, dorsal surface to the right. Fig. 27. Male tail from the lateral aspect. Fig. 28. Details of spicules and gubernaculum from the lateral aspect. (Figs. 21 and 26 ; 23 and 27 ; 25 and 28, to same scale.)

phageal teeth. There is one small, solid (?) tooth developed from each ventro-lateral sector and a large, hollow S-shaped dorsal tooth (Text-fig. 26). In addition there is a series of denticles, apparently developed along the anterior edge of the ventral radius of the oesophageal lumen and also along the more ventral of the edges of the dorso-lateral radii. Whether such a series is also present along the dorsal edge of the dorso-lateral radii is not clear but probably it is not since the dorsal tooth appears to be due to a thickening of the cuticle along the inner edge of the dorsal sector while the ventro-lateral teeth appear to be due to the thickening of the cuticle at the apex only of each ventro-lateral sector.

Tail

The tail is relatively long and thin with a very long, narrow spinneret (Text-figs. 25 and 27).

Male

The spicules are fairly strongly curved and are roughly the same width along most of their length. Anteriorly there is a distinct swelling for the attachment of the retractor muscles and just posterior to this the spicule narrows rather suddenly. The posterior ends of the spicules are bluntly rounded. The spicules appear to bear thin alae running from the tip to the point near the anterior end where the shaft suddenly narrows but this is uncertain. The gubernaculum is simple (Text-fig. 28). There is one testis with a distinct seminal vesicle (Text-fig. 24).

Female

There are two opposed uteri but due to the poor condition of the specimens the arrangement of the ovaries could not be definitely determined although they appear to be reflexed. The eggs, of which the maximum number seen in one specimen is two, one in each uterus, are spherical, 0·028 mm. in diameter.

Discussion

Hypodontolaimus angelae appears to be most similar to *Hypodontolaimus geophila* (de Man, 1876) in possessing a gubernaculum without an apophysis and in having two longitudinal rows of large dots separated by bars. The shape of the spicules in *H. angelae* is different with the definite constriction near the anterior end, which is not present in *H. geophila*, and with bluntly rounded posterior tips, these being sharply pointed in *H. geophila*. These differences have been confirmed by comparing the specimens of *H. angelae* with some of *H. geophila*. The position is, however, complicated by the somewhat unsatisfactory nature of the classification within the subfamily Chromadorinae, particularly the separation of the genera *Hypodontolaimus* and *Dichromadora*. Wieser (1954*b*) separates them almost wholly on the shape of the dorsal tooth, S-shaped in *Hypodontolaimus* and not so shaped in *Dichromadora*. Such a character, although clear in a specimen with a large tooth, is not at all clear in species in which the tooth is small. While I recognize that a character is not invalid because it is difficult to establish, the published descriptions of the species which

Wieser distributes between these two genera do not convince me that this is a satisfactory basis for a classification. However I am unable to suggest a better grouping now but, because of this difficulty, I have also compared *H. angelae* with the species referred to *Dichromadora*. Among them *H. angelae* appears to be most similar to *D. punctata* Schuurmans Stekhoven, 1950. As Wieser (1954*b*) points out the description given by Schuurmans Stekhoven is poor but *H. angelae* differs from *D. punctata* in the shape and position of the amphids and the shape of the spicules.

Wieser (1954*b*) treats *Spilophora canadensis* Cobb, 1914 as a synonym of *H. geophila* but this I cannot accept. The description given by Cobb is insufficient to determine either the systematic position or the specific validity of his species and until specimens from a comparable locality have been studied *S. canadensis* should be considered a *species inquirendum.*

Polygastrophora omercooperi sp. nov.

Material Studied

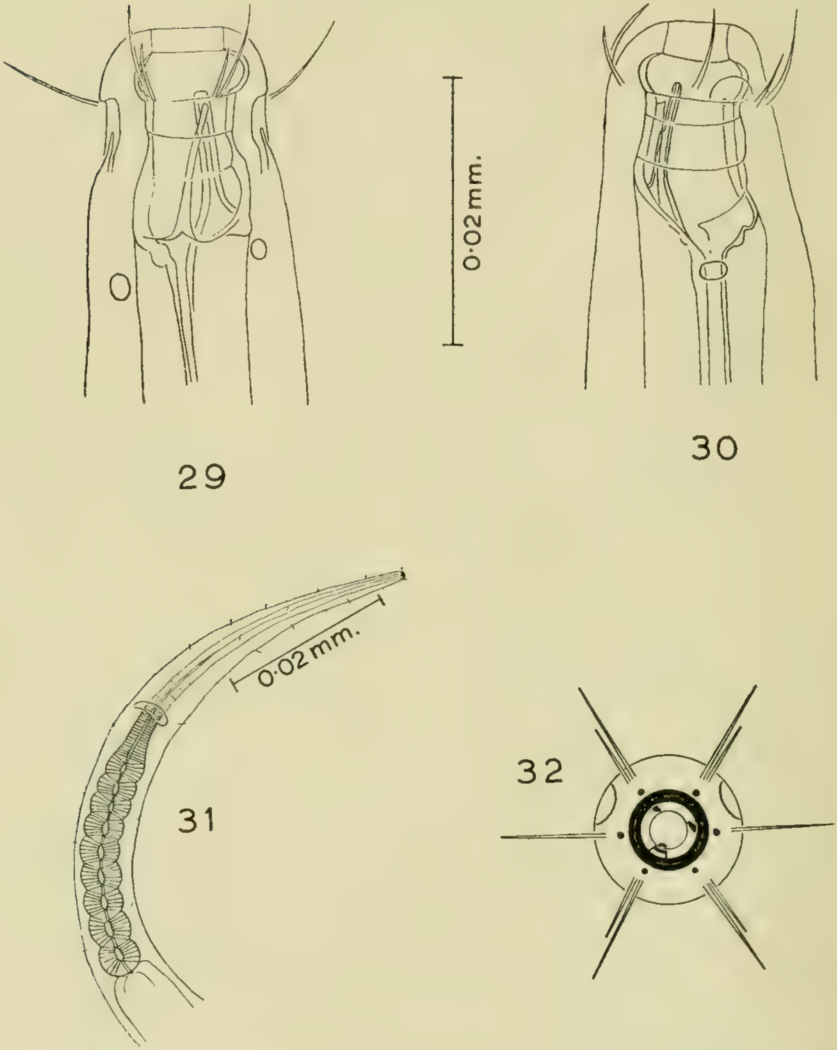
15 ♂ (1 without a head); 7 ♀ (1 immature); 1 4th stage ♀ larva. B.M. (N.H.), Reg. Nos. 1960, 273–296. Holotype ♂ selected, 1960, 273.

Proportions and Measurements (mm.)

	a	*b*	*c*	V	Body length
♂♂	34·4	4·5	17·8	—	3·24
	35·4	5·1	16·1	—	2·90
	32·1	4·1	15·0	—	2·60
	36·7	5·2	16·3	—	3·30
	37·0	4·5	17·8	—	3·55
♀♀	32·0	4·7	15·7	52·5	3·14
	34·3	4·1	14·7	59·6	2·92
	31·1	4·2	16·0	55·7	3·05
	32·4	4·9	15·4	56·2	3·13

Males (measurements in order of body lengths): Oesophagus length: 0·72; 0·59; 0·63; 0·64; 0·79. Buccal cavity depth: ——; ——; 0·017; 0·016; 0·018. Buccal cavity width: ——; ——; 0·005; 0·006; 0·006. Refractive bodies from anterior end: ——; ——; 0·018; 0·016; 0·019. Nerve ring from anterior end: ——; ——; 0·278; 0·340; 0·371. Excretory pore from anterior end: only seen in the 3·55 mm. long specimen, 0·077. Tail length (tail length/anal diameter): 0·186 (3·5); 0·180 (——); 0·173 (3·4); 0·203 (4·2); 0·199 (3·8). Spicule length: 0·28; 0·26; 0·26; 0·26; 0·28. Gubernaculum length: 0·045; 0·039; 0·041; 0·036; 0·046.

Females (all measurements in order of body lengths): Oesophagus length: 0·67; 0·72; 0·74; 0·64. Buccal cavity depth: 0·016; 0·015; 0·016; 0·016. Buccal cavity width: 0·006; 0·005; 0·006; 0·007. Refractive bodies from anterior end: 0·018; 0·019; 0·019; 0·019. Nerve ring from anterior end: 0·041; 0·039; 0·036; 0·038. Excretory pore from anterior end: 0·074; 0·072; ——; 0·074. Tail length (tail length/anal diameter): 0·200 (4·1); 0·191 (4·0); 0·198 (4·3); 0·203 (3·9). Vulva from anterior end: 1·65; 1·70; 1·74; 1·76.



Figs. 29–32. *Polygastrophora omercooperi* sp. nov. Fig. 29. Dorsal view of female head. Note the recessed amphids. Fig. 30. Lateral view of female head, dorsal side to the right. Fig. 31. Lateral view of the oesophagus, note nine bulbs. Fig. 32. *En face* view of female head. Note large tooth is right ventro-lateral in position. (Figs. 29, 30 and 32 to the same scale.)

Head and Oesophagus

The anterior end of the body narrows rapidly from about the posterior end of the oesophagus forward so that the head, in spite of the length of the body, is small, 0·010–0·011 mm. in diameter. There are many setae scattered over the anterior end of the body but they become progressively less common posteriorly until they are very rare posterior to the nerve ring. The mouth opening is circular, 0·004 mm. in diameter (in a male specimen 3·30 mm. long) and leads into a typical long, relatively narrow buccal cavity with parallel sides, except for the first chamber which is wider than the posterior chamber. The first chamber is 0·007 mm. in diameter, the second is 0·006 mm. The buccal cavity is divided into four parts by transverse rings, one at the opening of the swollen anterior chamber, one at the junction of that chamber and the narrower posterior chamber and two in the narrow chamber itself (Text-figs. 29 and 30). The small size of the head makes study difficult so that although small teeth appeared to be present on all three of the more anterior rings—on only one ring in some specimens, on two in others and on all three in some—I cannot be sure that they are a constant character of the species or whether in fact the serrated appearance is not an artifact. The transverse rings are therefore shown untoothed in the figures of the head (Text-figs. 29 and 30). Three teeth are developed from the base of the second chamber of the buccal cavity. The largest springs from the right ventro-lateral sector and the other two, which are much less prominent and equal in length, spring from the left ventro-lateral and the dorsal sectors of the oesophagus. Although in the *en face* figure of the head (Text-fig. 32) the dorsal tooth appears to be dorso-lateral in position and the left ventro-lateral appears to be lateral this is due to a slight spiralling of the teeth as they pass anteriorly. This is shown in the figure of the head from the dorsal aspect (taken from a different specimen from that used for the *en face* preparation) where it can be seen that their origins are wholly dorsal and ventro-lateral. The transverse rings appear to represent, from the anterior end to the posterior end (1) the junction of the mouth with the expanded anterior chamber; (2) the junction of the expanded chamber with the narrow chamber; (3) the level at which the dorsal and left ventro-lateral teeth become free at their anterior ends from the wall of the narrow chamber and (4) the level at which the large right ventro-lateral tooth becomes free from the narrow chamber. It follows from this that, as described above, there are only two true chambers the other rings only being apparent from certain angles as has been confirmed by rolling some of the specimens. This probably explains some of the discrepances between some of the descriptions of the species of this genus.

The mouth is surrounded by six small, sessile papillae and the head bears five pairs of long setae which originate about the level of the junction between the anterior and posterior chambers of the buccal cavity. Of these setae three pairs are long, 0·008 mm. in all the specimens measured, and two pairs are short, about 0·006 mm. The distribution of the setae is most easily understood from the figure (Text-fig. 32). The amphids are located about the level at which the cephalic setae originate and are dorso-lateral in position. They are semi-circular recesses which lead into pouches at the bases of which are the amphidial nerves (Text-figs. 29 and 30).

The oesophagus (Text-fig. 31) is very narrow anteriorly without any muscle bands which only become obvious just anterior to the nerve ring. Approximately the posterior third of the oesophagus is developed into nine bulbs each of which contains a central lenticular cuticularization from which radiate stands of muscles. In some specimens a tenth, very small and poorly developed bulb appears to be present but it is probably that this is simply an artifact.

The usual pair of lenticular refractive bodies is present about the posterior end of the buccal cavity. The bodies show some variation in their positions relative to the buccal cavity, both from specimen to specimen and between the two sides of the same specimen but in no case were they seen anterior to the posterior end of the buccal cavity.

Male

All the specimens appear to be larvae (4th stage : but see below, page 312) since the structure of the head is identical with that of the female. The tail is relatively long and the three caudal glands are located relatively far anterior to the cloacal opening. The spicules are long and narrow, equal in length and identical in structure. There is a small, simple gubernaculum. Anterior to the cloacal opening, on the ventral surface of the body, are six pairs of relatively evenly spaced papillae, although in some specimens they are further apart anteriorly than posteriorly. Also anterior to the cloacal opening is a series of oblique muscle strands running from the dorsal to the ventral surface of the body over a length of 0·89–0·92 mm. from the cloacal opening. There are two opposed testes, which are restricted to the anterior half of the body, and a heavily muscled ejaculatory duct.

Female

The tail is similar in outline to that of the male. There are two opposed uteri which are not (?) reflexed. The eggs are 0·041 × 0·024 mm. to 0·043 × 0·025 mm. in size and the greatest number seen in one specimen was one in each uterus.

Discussion

Polygastrophora omercooperi is distinct from all the other species referred to the genus by the presence of nine bulbs in the posterior end of the oesophagus.

Wieser (9953*a* and *b*) suggests that all the genera referred to the subfamily Enchilidiinae may be characterized by sexual dimorphism and points out that it is definitely known to occur in three of the genera of that subfamily, one of the genera in question being *Polygastrophora*. However, I find it difficult to believe that all the male specimens I have seen are fourth stage larvae as in many of them the reproductive organs appear to be fully developed and the spicules are frequently protruded from the cloacal opening. In addition it is difficult to believe that among nineteen male specimens found in association with gravid females none of the males is fully adult but that many of them are fourth stage larvae just about to moult to the adult condition. I therefore suggest that it is more probable that sexual dimorphism, involving a highly modified head in the male, does not necessarily occur in all the species of the genus *Polygastrophora* but only in some of them. In fact such a male is only known in *P. quinquebulba* Micoletzky, 1930.

Allgén (1959) describes a new species of *Bolbella*, *B. cylindricauda*, based on one female specimen. Although the description is extremely poor, without measurements other than a statement of the length of the body and the values of *a*, *b* and *c* ("The vulva was not to be stated."), it is clearly a species of *Polygastrophora* since Allgén refers to " light-refracting small bodies behind the buccal cavity ". Such bodies are characteristic of *Polygastrophora* but do not occur in *Bolbella* as Wieser points out (1953*b*, p. 132). Further Allgén draws attention to the similarities between his new species and the redescription of *Polygastrophora hexabulba* (Filipjev, 1918)—which Allgén attributes to Wieser—given by Wieser (1953*b*). While acknowledging that Allgén's description is insufficient and that his figures are virtually impossible to analyze, I have little doubt that *B. cylindricauda* is the same species as that described by Wieser as *P. hexabulba*, since the characters on which Allgén considers them distinct are such as could be due to poor preservation. Certainly the figure of the tail (Allgén, 1959, fig. 83*c*) could only have been drawn from a distorted specimen. I therefore propose that *B. cylindricauda* Allgén, 1959 be treated as a synonym of *P. hexabulba* (Filipjev, 1918).

Sphaerolaimus anterides sp. nov.

Material Studied

0 ♂; 4 ♀ (2 adult, 2 4th stage larvae). B.M. (N.H.), Reg. Nos. 1960.300–303. One adult female selected as Holotype, 1960.300.

Proportions and Measurements (*mm.*)

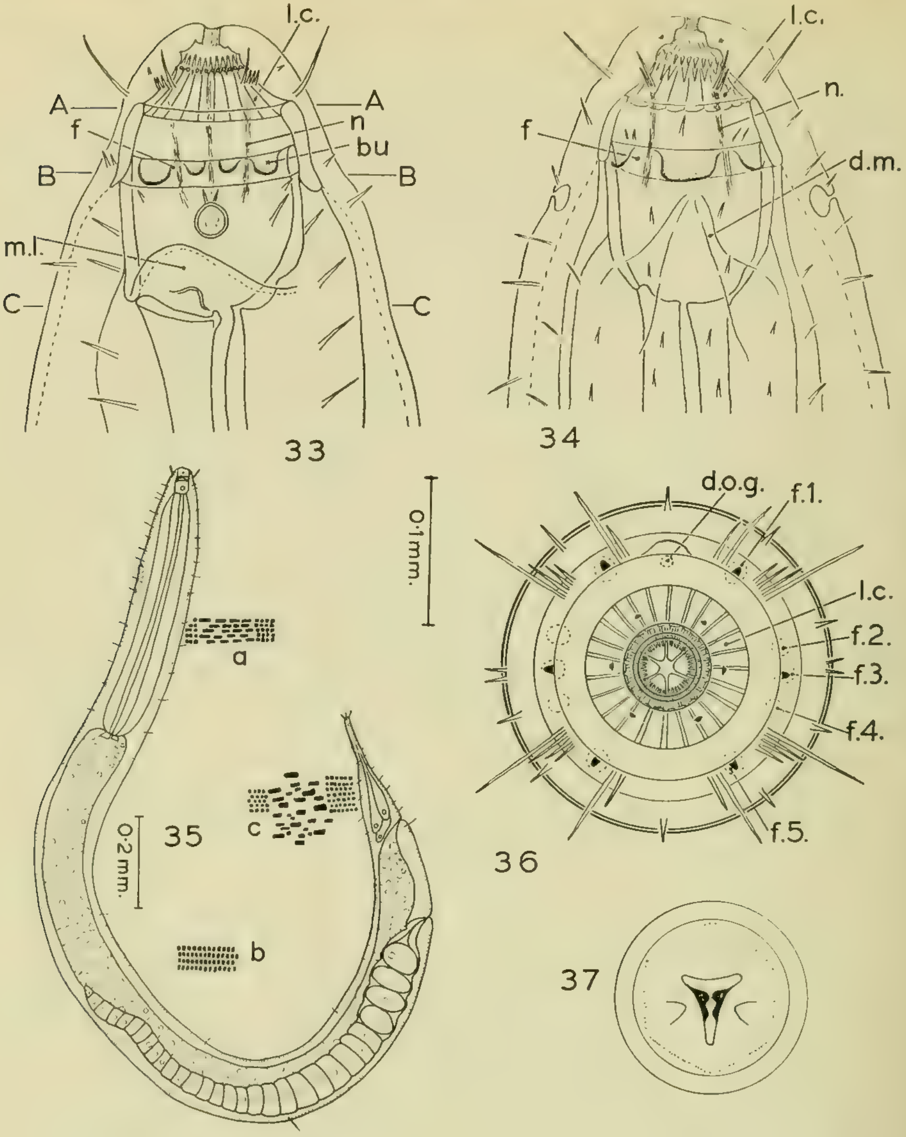
a	*b*	*c*	V	Body length
19·7	4·0	9·9	82·8	2·38
19·6	4·6	10·5	83·2	2·74
16·4	3·9	9·7	83·3	1·74 (larva)

Adult (in order of body lengths) : Oesophagus length : 0·59 ; 0·59. Head diameter at "A" (see Text-fig. 33) : 0·041 ; 0·037, at "B": 0·057 ; 0·053, at "C": 0·068 ; 0·071. Amphid diameter (percentage of corresponding head diameter) : 0·006 (10·5) ; 0·006 (11·3). Buccal capsule diameter : 0·027 ; . . . . Buccal capsule depth : 0·015 ; . . . . Nerve ring from anterior end : . . . ; 0·19. Excretory pore from anterior end : 0·21 ; . . . . Tail length (tail length/anal diameter) : 0·24 (3·1) ; 0·26 (3·8) Vulva from anterior end : 1·97 ; 2·28.

Larva : Oesophagus length : 0·45. Head diameter at "A" : 0·037, at "B": 0·050, at "C": 0·061. Amphid diameter (percentage of head diameter) : 0·007 (14·0). Nerve ring not seen. Excretory pore from anterior end : 0·18. Tail length (tail length/anal diameter) : 0·18 (2·1). Vulva from anterior end : 1·45.

Cuticle

The cuticle bears very fine, close-set transverse striations, about 0·001 mm. apart, over most of the body, which resolve into series of small rectangular blocks (Text-fig.



Figs. 33–37. *Sphaerolaimus anterides* sp. nov. Fig. 33. Lateral view of head. Dorsal side to the right. Fig. 34. The same from the dorsal surface. Fig. 35. Whole body. Note posterior position of vulva and only one ovary. *a* = cuticular markings on anterior end of body. *b* = cuticular markings on middle part of body. *c* = irregular markings about level of anus (semi-diagrammatic). Fig. 36. *En face* view of head. Fig. 37. Optical section through oesophageal funnel showing ventro-lateral teeth. (Figs. 33, 34, 36 and 37 to the same scale.) (A——A, B——B and C——C indicate levels referred to in the text. l.c. = leaf crown; n = nerves supplying cephalic sense organs; bu = buttresses of buccal capsule; f = foramina; m.l. = muscular lobes developed on the ventro-lateral sides of the oesophageal funnel; d.m. = dorsal muscle fibres of oesophageal funnel; d.o.g. = duct of dorsal oesophageal gland; f_1–f_5 = foramina.)

35, *b*). The markings start anteriorly about the level of the anterior edge of the buccal capsule (Text-fig. 33, level "A") where they are regular and slightly more elongate than those on the major part of the body. More posteriorly, particularly around the amphid, the blocks on the lateral fields become longer, more prominent and slightly irregular both in shape and distribution (Text-fig. 35, *a*), although never to the same extent as the markings on the posterior end of the body (see below). This anterior zone of larger markings continues posteriorly, narrowing evenly until it disappears about the level of the posterior end of the oesophagus, the smaller blocks flanking the lateral zone becoming smaller and squarer concomitantly. On the posterior end of the body, about the level of the anus, the regular arrangement is also lost and is replaced by blocks along the lateral fields which are very irregular in arrangement and shape. The area so covered is V-shaped with the wider part anteriorly. The regular arrangement persists dorsally and ventrally (Text-fig. 35, *c*).

There are many longish setae, about 0·006 mm. long, arranged in sixteen evenly spaced files. The setae are relatively close together anteriorly but become further apart posteriorly until they cease about the level of the posterior end of the oesophagus The remainder of the body bears only a few setae but they become more frequent again on the tail (Text-fig. 35).

Head and Oesophagus

The head bears two circles of six sessile papillae of which those of the inner circle are small and inconspicuous while those of the outer are fairly prominent, but are not setiform (Text-fig. 36). Slightly posterior to the outer circle of papillae is a circle of four sets of setae of which one seta is much longer (0·012-0·013 mm. on the adults 0·011 mm. on the larvae) than the other three and is the most lateral in all four groups. The other three setae are of different lengths, becoming shorter the more dorsal or ventral (depending on the group to which they belong) their position. These four groups are dorso- and ventro-lateral in position (using the terminology of de Coninck (1942) and Hyman (1951), p. 201, fig. 94). Immediately posterior to this circle is another, also consisting of four groups of setae, but of only two setae per group. In this case also the more lateral seta is longer than the other in each group. There are further small setae which appear to correspond to those covering the general surface of the anterior end of the body except that the first circle consists of eight setae instead of sixteen as on the remainder of the body. In addition there are two small setae immediately anterior to each amphid.

The mouth opening is circular in shape and is closed by six fleshy lip-lobes which appear to be striated radially, but it is possible that this appearance is due to the underlying longitudinal striations of the cavity anterior to the leaf elements (= vestibule) (see below). The mouth leads through the vestibule into a capacious, globular buccal cavity which is bordered anteriorly by a set of leaf elements forming a leaf crown (I am applying the terminology used in the strongyloids, a group of parasitic nematodes, see below, page 317). Posterior to the leaf crown the buccal cavity consists of two distinct parts the more anterior of which, between levels "A" and "B" (see Text-figs. 33 and 34) will be referred to as the buccal capsule while the more posterior will be referred to as the oesophageal funnel (another term applied to the strongyloids). The buccal capsule is circular in cross section and the leaf crown (Text-fig. 36, l.c.) is composed of twenty five leaf elements which arise as thin cuticular strips from the inner surface of the buccal capsule just posterior to its extreme anterior edge. Anterior to the leaf crown there appears to be a second leaf crown consisting of much smaller leaf elements but this effect is due to the longitudinal folding of the cuticle lining the vestibule whih produces longitudinal striations (see Cobb, 1929). The posterior end of the buccal capsule lies over the wall of the oesophageal funnel as twelve " buttresses " (Text-figs. 33 and 34, *bu*) which are the only sclerotized parts of the buccal capsule i.e. they show up distinctly even under very low powers and appear to be covered by small dots. These buttresses are extremely prominent and appear to be characteristic of this species. Further, the buccal capsule is fused to the body wall by these butttresses and the nerves which supply the cephalic setae and papillae can be seen passing through the spaces between them (" *n* "). These spaces are represented on the *en face* view of the head (Text-fig. 36) by somewhat oval spaces enclosed by dashes (" *f* "), since this is the impression they give, although a more detailed study shows that they are in fact bounded internally by the buccal capsule and/or the wall of the oesophageal funnel and externally by the cuticle covering the body. The oesophageal funnel is massive and appears to be divided into two parts. There are two well developed teeth at the base of the funnel, one on each ventro-lateral sector (Text-fig. 37). There is no corresponding tooth dorsally but there is a marked thickening of the dorsal wall of the oesophageal funnel through which passes the duct of the dorsal oesophageal gland (Text-fig. 36, *d.o.g.*). The musculature of the ventro-lateral sectors of the oesophagus continues anteriorly as two lobes (Text-fig. 33, *m.l.*) which stop about the middle of the oesophageal funnel. There are no lobes dorsally although there is a slight development of muscles in two separate blocks (Text-fig. 34, *d.m.*). The oesophageal funnel is circular in cross section anteriorly but becomes hexagonal in cross section internally towards the bottom (Text-fig. 37).

The amphids lie anterior to the base of the oesophageal funnel, roughly half way between the posterior and anterior ends. They are circular in outline and the opening is a small circle leading into a larger cavity. Most figures show only a large circle which may have been due to the authors overlooking the small circle of the opening, but there may in fact be a difference in the form of the amphids. The amphidial nerve appears to enter from the posterior side but a slight break in the outer periphery in one specimen suggests that the nerve may in fact enter from the dorsal side, but I cannot be sure owing to the difficulty of seeing the nerves.

The oesophagus is stout without a posterior swelling and is lined by thick cuticle along its whole length.

Tail

The tail narrows suddenly about two-thirds of its length posterior to the anus and bears several rows of relatively long setae. There are three very distinct, stout setae on the extreme tip of the tail which are about 0·014 mm. long in the adults and 0·009 mm. long in the larvae. The three caudal glands are located immediately posterior to the anus (Text-fig. 35).

Reproductive Apparatus

There is a single ovary which is not reflexed and there does not appear to be a distinct oviduct. The eggs, of which the greatest number seen in one specimen was four, measure 0·063 × 0·051 mm. and 0·069 × 0·056 mm. The vulva lies relatively far posterior to the head, $V = 83$, and there is no post-vulvar sack (Text-fig. 35).

Discussion

Sphaerolaimus anterides belongs to what may be called the Parasphaerolaimus-group of the genus *Sphaerolaimus*, a group characterized by a reduced buccal capsule (in the nomenclature used here ; " sclerotized portion " of Wieser (1956) ; " chagrinierter Teil " in German literature ; " chagrinated cuticularized plates " of Schuurmans Stekhoven (1950)). This group contains three species, according to Wieser (1956), *S. dispar* Filipjev, 1918 ; *S. paradoxus* Ditlevsen, 1919 and *S. islandicus.* Ditlevsen, 1926 ; from all of which *S. anterides* differs in the form of the buccal capsule, perhaps in the presence of cuticular differentiation on the body (this character is doubtful since such markings may have been overlooked) and, apparently, in the length and distribution of the cephalic setae. The position is complicated, however, by the unsatisfactory nature of some of the descriptions and figures. One further species referable to the Parasphaerolaimus-group has been described since Wieser, *S. lodosus* Gerlach, 1954. Gerlach's full description brings out the many resemblances between his species and *S. anterides* but they differ in the cuticular pattern and the structure of the buttresses of the buccal capsule.

The use of the terms " leaf crown " and " oesophageal funnel " is not to be taken as indicating any homology between the structures so named in *Sphaerolaimus* and in the strongyloids. They are used solely as descriptive terms since there is a marked similarity in appearance between the two head forms. Such descriptions are used in preference to more specific terms such as cheilorhabdions, a term employed by Chitwood (in Chitwood and Chitwood, 1951) and by Wieser (1956) for what are referred to above as leaf elements, since such a term carries a concept of homology which may be unfounded and certainly is not satisfactorily established.

The great depth and diameter of the buccal cavity (i.e. the entire cavity stretching from the mouth opening to the posterior end of the oesophageal funnel) must introduce serious mechanical weaknesses which have been overcome by the attachment of the buccal capsule to the body wall by means of the buttresses. Since some provision must be made for the passage of the nerves which supply the sense organs of the head this fusion is incomplete leaving ten foramina (Text-figs. 33, 34 and 36, *f*) through which the nerves pass. The foramina being flanked by the buttresses. Thus the nerves which supply the four sets of four setae pass through the dorsal and ventral foramina of each lateral set of three (*f*2 and *f*4, Text-fig. 36). The nerves which supply the four sets of two setae pass through the dorso- and ventro-lateral foramina (*f*1 and *f*5) and the nerves which supply the dorso- and ventro-lateral papillae of the inner and outer circles pass through the same foramina (i.e. *f*1 and *f*5) while the nerves supplying the lateral papillae of both circles pass through the lateral foramina (*f*3). Several minor nerves supplying the various supernumerary setae of the head also pass through the foramina. Such foramina appear to be present in all species of *Sphaerolaimus* but appear to be much more prominent in the species of the Parasphaerolaimus-group (see, for example, Schuurmans Stekhoven (1950), figs. 127 and 128 ; Gerlach (1954) Tafel XVII, Abb. 24*a*, *b*, *c* ; and Filipjev (1918) figs. 69*a*, *b*, *f*). The foramina should not, however, be confused with the fenestrae which occur in some of the species of the Sphaerolaimus-group of species and which appear to represent a tendency towards the lightening of the buccal capsule.

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THE SPECIES OF *RHABDITIS* (NEMATODA) FOUND IN ROTTING SEAWEED ON BRITISH BEACHES

By WILLIAM G. INGLIS AND JOHN W. COLES

SYNOPSIS

Rhabditis marina Bastian, 1865, is reported from several localities on the South Coast of England and from Aberdeen, Scotland. Although this species has been reported from several localities in Europe and in North and South America these are the first records of its occurrence in Britain since it was originally described from Falmouth. *Rhabditis ehrenbaumi* Bresslau and Schuurmans Stekhoven, 1935, originally reported from Heligoland, is reported from the South and West Coasts of England and Wales : these are the first records of this species since the original description. Both species are fully redescribed and none of the varieties of *Rh. marina* which have been described or named are accepted with the exception of *Rh. m.* var. *bengalensis* Timm, 1956, which is considered to represent a distinct species *Rh. bengalensis*. *Rh. m.* var. *nidrosiensis* Allgén, 1933, is considered to be a *nomen dubium*. *Rh. velata* Bresslau and Schuurmans Stekhoven, 1935, is considered to be a synonym of *Rh. marina* and further evidence is presented supporting the treatment of *Rh. fluviatilis* Bütschli, 1876, as a synonym of *Rh. marina*. The occurrence of *Rh. marina* is discussed and it is considered to be a form which, although found away from beaches, must be considered a normal member of the beach fauna, typically occurring in rotting seaweed and that its occurrence in beach pools must be considered accidental. It is suggested, tentatively, that *Rh. ehrenbaumi* is probably not a typical beach form but insufficient is known about its distribution for any definite conclusions to be drawn.

THE species of *Rhabditis* most frequently reported from marine habitats is *Rhabditis marina* which was described by Bastian (1865) from specimens found in sand from tide-pools at Falmouth, England. Subsequently six varieties of this species have been described or named, and it has been reported, in one form or another, from the coasts of Europe, the Atlantic coast of the United States of America, the coast of Brazil, the coast of Pakistan, from the South Pacific (Campbell Island) and from the Falkland Islands. It has not, however, been reported from the coast of Britain since the original description. Although we have been unable to find it at Falmouth, we have found specimens at several localities on the South and West Coast of England and have received specimens from Scotland. A full redescription of *Rh. marina* is given below and we are able to demonstrate that some at least of the characters used to differentiate the various varieties are simply due to intraspecific variation.

Two further "marine" species of *Rhabditis* (*Rh. ehrenbaumi* and *Rh. velata*) were described by Bresslau & Schuurmans Stekhoven (in Schuurmans Stekhoven, 1935 ; Bresslau & Schuurmans Stekhoven, 1940) from Heligoland and neither has been reported since. We have found specimens of the first species on the South and West Coast of England and the South Coast of Wales and a redescription of it is given below. One male specimen which at first sight appeared to belong to the second species was received from Scotland, but a detailed study demonstrated that the apparently distinguishing characters were in fact due to poor preservation and we consider *Rh. velata* a synonym of *Rh. marina*.

Rhabditis (Pellioditis) marina Bastian, 1865

Synonymy :

Rhabditis marina Bastian, 1865. *Trans. Linn. Soc. Lond.* **25**, 129. Pl. 10, Figs. 60–62.
Rhabditis fluviatilis Bütschli, 1876. *Z. wiss. Zool.* **26** : 365. Taf. XXIV, fig. 8.
Rhabditis marina var. *septentrionalis* Steiner, 1921. *Zool. Jb.* (Syst. etc.) **44** : 10 (= *Rh. marina* of Steiner, 1916. *Zool. Jb.* (Syst. etc.) **39** : 518. Taf. 18, figs. 1*a–g*.)
Rhabditis marina var. *kielensis* Schulz, 1932. *Zool. Jb.* (Syst. etc.) **62** : 419. Fig. 49*a–e*.
Rhabditis marina var. *danica* Allgén, 1933. *Capita Zool.* **4** : 123 (= *Rh. marina* of Ditlevsen, 1912. *Vidensk. Medd. naturh. Foren. Kbh.* **64** : 240. Pl. II, figs. 1–5, 7.)
Rhabditis velata Bresslau & Schuurmans Stekhoven, in Schuurmans Stekhoven, 1935. *Tierwelt N. -u. Ostsee.* **5** : 155. Fig. 338.
Rhabditis (*Choriorhabditis*) *fluviatilis*, Osche, 1952. *Zool. Jb.* (Syst. etc.) **81** : 263.
Rhabditis (*Choriorhabditis*) *velata*, Osche, 1952. *Zool. Jb.* (Syst. etc.) **81** : 264.
Rhabditis (*Caenorhabditis*) *marina*, Osche, 1952. *Zool. Jb.* (Syst. etc.) **81** : 265.
Rhabditis (*Choriorhabditis*) *marina marina*, Osche, 1954. *Zool. Anz.* **152** : 247.
Rhabditis (*Pellioditis*) *fluviatilis*, Dougherty, 1955. *J. Helminth.* **29** : 131.
Rhabditis (*Pellioditis*) *velata*, Dougherty, 1955. *J. Helminth.* **29** : 131.
Rhabditis (*Pellioditis*) *marina*, Dougherty, 1955. *J. Helminth.* **29** : 132.
nec *Rhabditis* (*Choriorhabditis*) *marina* var. *bengalensis* Timm, 1956. *J. Bombay nat. Hist. Soc.* **54** : 87. Figs. A and B (= *Rh. bengalensis*).

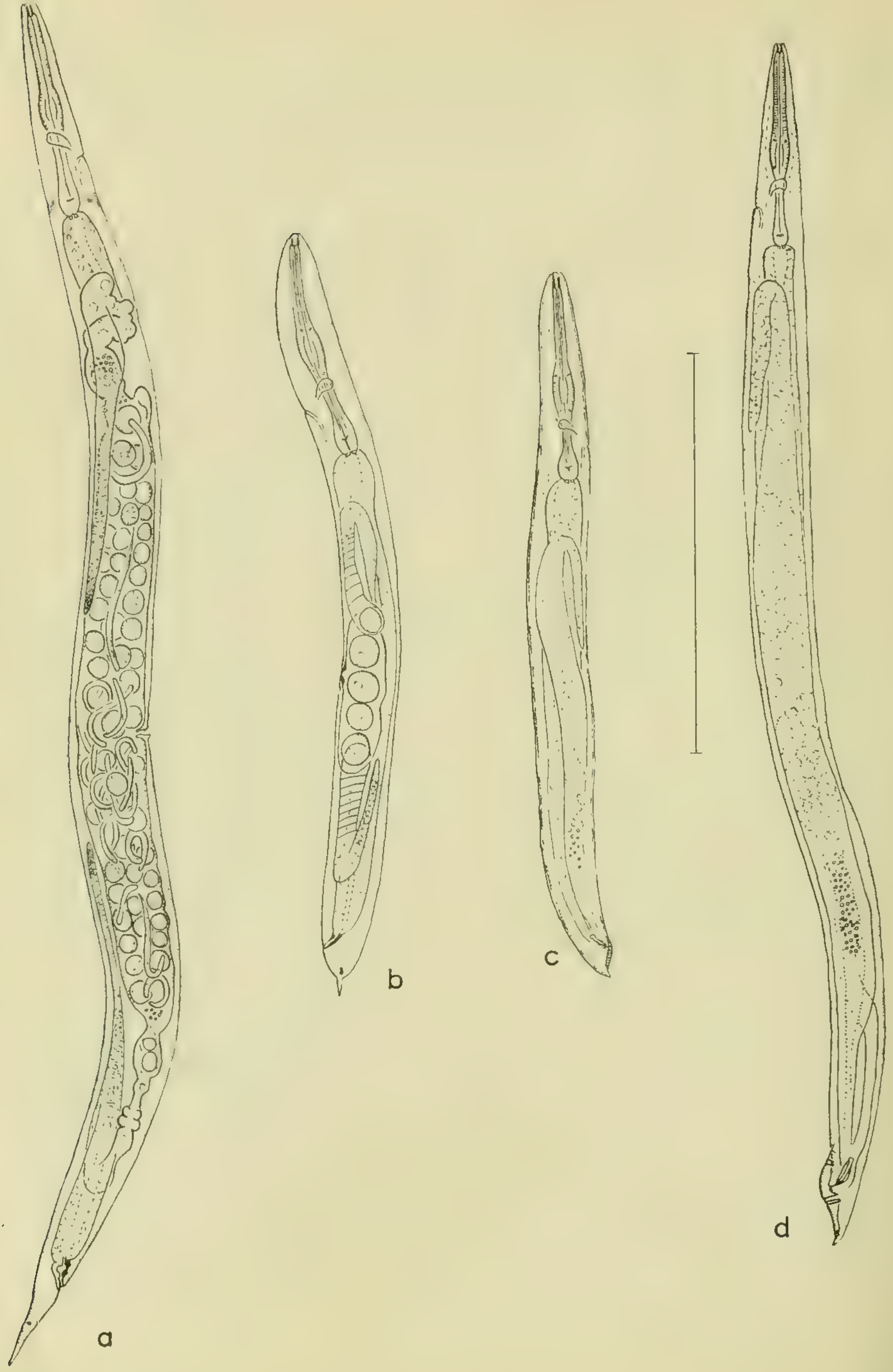
Type locality: In sand from tide-pools, Falmouth, south coast of England.

Material studied

Fifty-nine specimens (B.M. (N.H.) Reg. Nos. 1958.12.5.31–60; 1960.2–30) from rotting sea-weed on beach at Downderry, Cornwall (11 ♂, 11 ♀ measured). Other specimens have been studied, but not measured, from the following localities: Littlehampton, Sussex; West Wittering, Sussex; Parson and Clerk Rock, nr. Holcombe (between Dawlish and Teignmouth), Devon; Sunny Cove, East Portlemouth (Salcombe Estuary), S. Devon; Sennen Cove, Sennen (near Land's End), Cornwall (larvae only); Weston-Super-Mare, Somerset; Aberdeen, Scotland. All these specimens were found in association with rotting sea-weed.

Geographical distribution

Barents Sea (Steiner, 1916); Denmark, coast of (Ditlevsen, 1912); Germany, Baltic coast (Schulz, 1932); Kiel Bay, Germany (Otto, 1936; Gerlach, 1954*a*); Ostend (De Coninck & Schuurmans Stekhoven, 1933) and Zeebrugge (Schuurmans Stekhoven, 1935*a*), Belgium; West Sweden (Allgén, 1950); Heligoland, North Sea (Bresslau & Schuurmans Stekhoven, 1940); Mediterranean—Italy and Algeria (Osche, 1954); Coast of Algeria (Gerlach, 1954*b*); Woods Hole (Timm, 1956) and Long Island, N.Y., Atlantic Coast of the U.S.A. (Chitwood, 1951); Pernambuco, Brazil (Gerlach, 1956); ? Campbell Island, South Pacific (Allgén, 1932); Falkland Islands, Port William (Allgén, 1959); Falmouth (Bastian, 1865), and other localities


a
b
c
d

in England and Scotland listed above (present authors). Several localities (not beaches) in Germany (Bütschli, 1876; Hirschmann, 1952; Meyl, 1955) and from Hungary (Andrássy, 1958).

Measurements (specimens fixed in " Taf " and mounted in glycerine).

Males—(n = 11). *L.* = 1·40–1·75 (1·59 ± 0·112). *a* = 13·2–23·8 (19·55 ± 3·03). *b* = 5·6–6·9 (0·43 ± 0·482). *c* = 17·6–23·4 (20·20 ± 2·12).

Females—(n = 11). *L.* = 1·61–2·42 (1·90 ± 0·262). *a* = 14·6–21·7 (18·5 ± 1·97). *b* = 6·2–8·6 (6·9 ± 0·89). *c* = 12·4–18·6 (15·2 ± 1·89). *V.* = 50–56 (53 ± 1·55).

MORPHOLOGY

General

The body is relatively narrow and terminates in a relatively long tail in both sexes; laterally it carries well defined lateral fields which have eight incisures about the middle part of the body length where the fields are about one fifth the diameter of the body in width. The oesophagus is typical of *Rhabditis* with a distinct middle bulb and a poorly developed posterior bulb, the valves of which bear a series of semi-elliptical concentric ridges. The oesophagus anterior to the middle bulb is markedly wider than the part posterior to that bulb.

Head

The head appears to carry a full complement of sixteen papillae which are arranged in three circles (Text-fig. 2*e*); two pairs, dorso- and ventro-lateral in position, in an outer circle; three pairs in an intermediate circle and (?) three pairs in an inner circle. The papillae of the outer and intermediate circles are setiform and have been seen very clearly particularly in some of the specimens from Scotland, but those of the inner circle appear to be sessile and it is not certain that they do in fact exist. The amphids are slightly dorso-lateral in position and are prominent with large openings (Text-fig. 2*e* and *f*). The mouth opening is bounded by six-lip-lobes which are not off-set from the body and are free from each other at their ends nearer the central axis of the body, but pass backwards onto the surrounding head where they form six prominences on which are located the papillae and the amphids. The buccal cavity (cheilostome) is circular in cross section and is divided anteriorly into six pointed processes, one of which corresponds with each lip-lobe. The prostome is triangular in cross section, this being the triangular structure shown in Text-fig. 2*e*. The metastome bears a series of five tubercle-like structures and the base of the stoma is surrounded by an oesophageal " sleeve ", i.e. muscular tissue extends anteriorly around the posterior part of the stoma.

Male

The tail is relatively long and narrow with broad caudal alae which continue round the posterior tip, i.e. the tail is *peloderan*. The alae are supported by nine

FIG. 1. *Rhabditis marina*, female containing eggs and larvae (*a*), male (*d*); *Rhabditis ehrenbaumi*, female (*b*), male (*c*). All figures to same scale. (Scale line = 0·5 mm.)

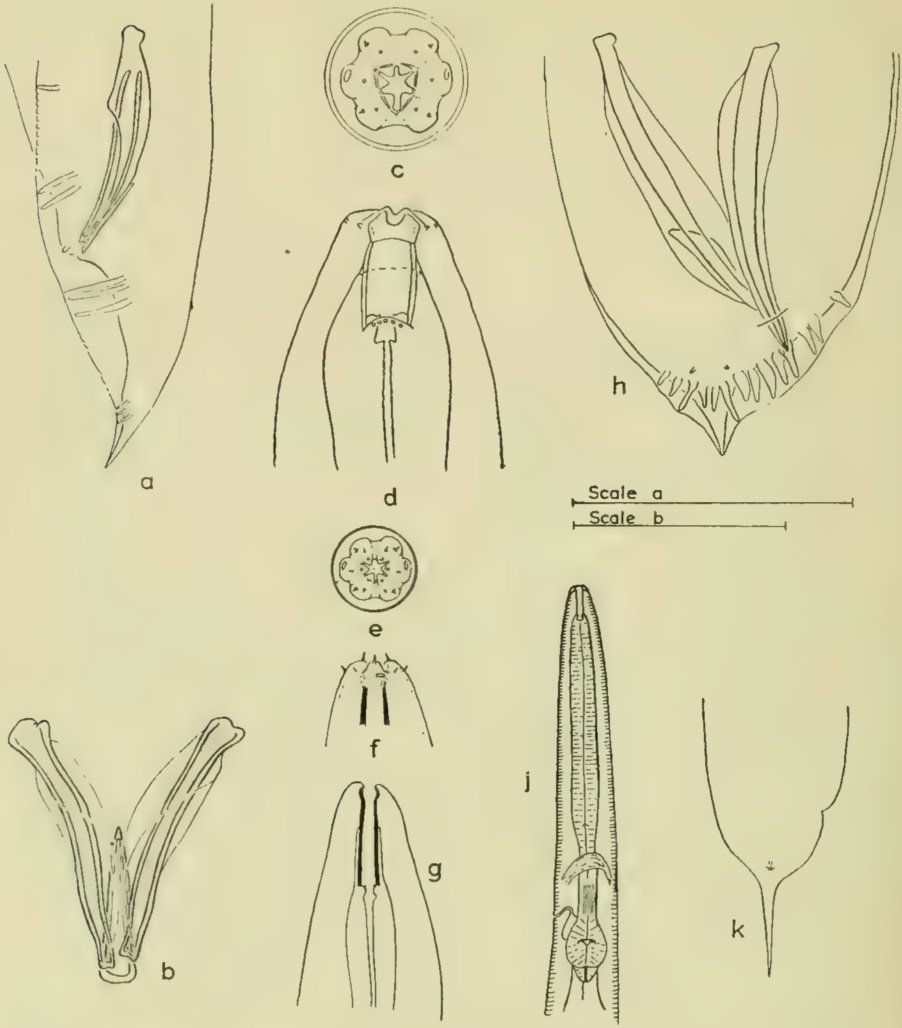


FIG. 2. *Rhabditis marina*, posterior end of male (lateral view) (*a*), ventral view of spicules and gubernaculum (*b*), *en face* view of head (♀) (*e*), lateral view of head with the dorsal surface to the right (*f*), optical section through buccal cavity and anterior end of oesophagus (*g*); *Rhabditis ehrenbaumi*, *en face* view of head (*c*), dorsal view of head showing five tubercules on the metastome (*d*), semi-ventral view of male tail showing the distribution of the caudal papillae in detail on one side only (*h*), posterior end of female (*k*); *Rhabditis bengalensis* sp. nov., structure of oesophagus (redrawn after Timm), note particularly the lack of a distinct median bulb (*j*). (*a*, *g* and *k* to same scale a; *b*, *c*, *d*, *e*, *f* and *h* to same scale, b; both scale lines = 0·05 mm.)

pairs of long narrow caudal papillae, or rays, arranged in definite groups: one pair far anterior, a group of two pairs mid-way between the most anterior pair and the cloacal opening, a group of three pairs very close together just posterior to the cloacal opening and a final group of three pairs just anterior to the posterior tip of the tail (Text-fig. 2*a*). The two anterior pairs of papillae in the more anterior group of three are very close together and can frequently be resolved only with great difficulty. The phasmids open on the ventral surface of the tail just anterior to the most posterior group of papillae. There is, in addition, at least one pair of sessile papillae on the anterior lip of the cloacal opening and possibily a second pair on the posterior lip. The spicules are equal in length, 0·40–0·70 mm., identical in structure and are not fused. They terminate posteriorly in " doubled " swollen ends (Text-figs. 2*a* and *b*) and bear broad double alae which are slightly folded over the main central shaft forming open tubes in all the specimens studied. The gubernaculum is broader posteriorly than it is anteriorly and is about half as long as the spicules. There is only one testis, which is flexed, and posteriorly there appears to be a pair of rather short ejaculatory glands.

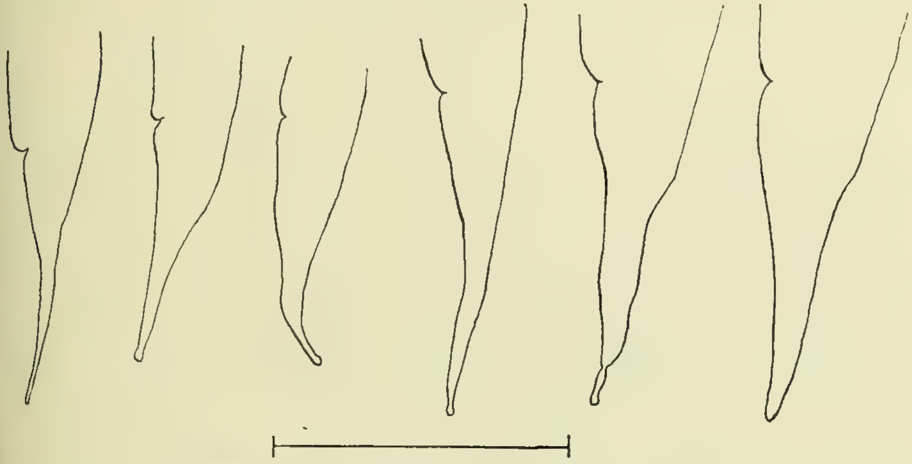


FIG. 3. *Rhabditis marina*, variation in female tail. (Scale line = 0·1 mm.)

Female

The vulva opens on the ventral surface of the body slightly posterior to the middle of the body length, *V* varying from 50–54%. The tail is long and somewhat variable in shape. It ranges from a very long, narrow form with a fine tip in the immature females to a relatively short stout form without such a tip in mature specimens. The range of variation is illustrated in Text-fig. 3 and it appears that as the width of the body increases with the appearance and development of eggs the tail becomes wider and shorter, with the result that a constriction appears slightly anterior to the end ; this is the tail form that Osche considered to be diagnostic of the subspecies *Rh. m. septentrionalis.* Finally the extreme posterior tip of the tail may become lost. The shape of the female tail has been used as the distinguishing character separating the two subspecies, *marina* and *septentrionalis* (see Osche, 1954), but it is clear that the reliance put on it has been misplaced. The reproductive system is amphidelphic and didelphic (as defined by Chitwood and Chitwood, 1950) (Text-fig. 1*a*). The ovaries are reflexed and there are short oviducts which are swollen just before the uteri to form large sacks which appear to function as spermathecae ; there is no indication of spermathecae in the uteri. The uteri are large ; in mature females they are packed with a large number of eggs and in the most mature specimens larvae are also present (Text-fig. 1*a*). The eggs are relatively small and spherical, 0·036–0·045 mm. in diameter.

Discussion

Six varieties of *Rh. marina* have been named of which one appears to represent a distinct species, one—possibly two—should be treated as a *nomen dubium* and the remaining four (or three) are indistinguishable, thus var. *danica* Allgén, 1933 (a name proposed for the description of *Rh. marina* given by Ditlevsen, 1912) has, according to the description, nine pairs of caudal papillae, or rays, on the male tail, arranged in groups of 2, 2, 3, 2 (from the figure of the lateral aspect) or 1, 2, 3, 2 (from the ventral view) ; var. *kielensis* Schulz, 1932 was described as having seven pairs arranged 1, 2, 3, 1 ; var. *nidrosiensis* Allgén, 1933 was proposed for one male specimen which apparently had seven pairs of papillae, but as the description is insufficient for identification we propose to treat this as a *nomen dubium* ; var. *norwegica* Allgén, 1933 was proposed for one female specimen which was probably a young female of *Rh. marina* and, in spite of the very poor description and figures, we propose to treat it as a synonym of *Rh. marina* (it might be better to treat this as another *nomen dubium*) ; var. *septentrionalis* Steiner, 1921 was a name proposed by Steiner for the specimens described by him in 1916 and was based on females only. The arrangement of the papillae on the male tail typical of *Rh. marina* is 1, 2, 3, 3, of which one of the pairs in the last group can be easily overlooked as has probably been done by Ditlevsen (1912) (we consider his lateral view of the male tail showing two papillae anteriorly to be faulty), Schulz (1932) and de Coninck and Schuurmans Stekhoven (1933) where fewer than three pairs of papillae are shown in the terminal group. Osche (1954) has suggested that these reported differences may represent natural variation but, while agreeing that this is possible, we feel it more probable that the papillae have simply been overlooked, particularly as we have found no variation in all the specimens we have studied.

Osche (1954) reviewed all the varieties and concluded that there were only two sub-groups which he treated as subspecies, *Rh. marina marina* and *Rh. m. septentrionalis.* He referred all the varieties listed above to the second sub-species which he considered to differ from the first in that the female tail ended in a relatively long, sharply pointed tip in *septentrionalis* and was stouter and blunter in *marina.* We agree with Osche that the various varieties are indistinguishable, with the reservation that var. *nidrosiensis* cannot be placed, but we cannot accept the separation into two subspecies. That such a separation is unacceptable is shown by the outlines of the female tails reproduced in Text fig 3 from which it can be seen that the range of variation includes both types of tail and also some which have not been graced with varietal names. We therefore recognize none of the varieties or subspecies and treat all the names proposed—with the exception of *Rh. marina* var. *bengalensis* (see below, page 327)—as synonyms of *Rh. marina.*

Rh. marina has been reported from many localities on the coasts of Europe and we have been able to find it almost everywhere we have looked on the South and West Coast of England (always in association with rotting sea-weed) while Mr. Douglas Bremner, who at our request looked for it at Aberdeen, had no difficulty in finding it there also. There are six reports of its occurance outside Europe, twice from the U.S.A. (Chitwood, 1951 ; Timm, 1956), once from the Southern Pacific (Allgén, 1932), once from the Falkland Islands (Allgén, 1959), once from the Bay of Bengal, Pakistan (Timm, 1956) and several times from the beach at Pernambuco, Brazil (Gerlach, 1956). Chitwood recorded one female from Long Island, N.Y., and Timm (1956) mentions that he found males at Woods Hole. Gerlach's specimens were identified by Dr. Arwed H. Meyl who has studied European specimens (see Meyl, 1955) and it cannot be doubted that *Rh. marina* occurs on both sides of the Atlantic Ocean. Allgén (1932) reported *Rh. marina* from Campbell Island, South Pacific (52° 34′ S. 169° 12′ E.) but the validity of the identification, which was based on one female specimen, must be considered very doubtful although Osche (1954) apparently accepts it. The record of *Rh. marina*, by the same author (Allgén, 1959), from the Falkland Islands appears to be slightly more reliable although the figure of the male tail is too poor to allow us to be certain.

The position of the remaining variety, *Rh. m. bengalensis* Timm, 1956 (referred to as *Pellioditis marina* var. *bengalensis*, n. comb. by Timm (1960)) is different. It was based on one male specimen (collected from " Sonadia Island, Cox's Bazar, Bay of Bengal, East Pakistan ") which Timm considered to be distinct in having nine pairs of caudal papillae arranged 1, 1, 1, 3, 3, since, as he rightly points out, the typical *marina* arrangement is with the second and third pairs (from the anterior end) very close together, while in his specimen they are far apart. This distribution is clearly shown in his figure. Also the figure of the oesophagus shows it to be different in outline from that typical of *Rh. marina*, so much so that we feel it probable that, unless the figure is completely inaccurate, Timm was dealing with a different species. The corpus of the oesophagus is the same width all along its length so that there is no distinct middle bulb (See Text-fig. *2j*—Timm's figure redrawn) and we feel that this, in conjunction with the distribution of the caudal papillae and the apparently sharp posterior points to the spicules (although this is possibly an unreliable character since Timm's figure of the male tail is clearly somewhat diagrammatic) warrants the treatment of this variety as a distinct species, *Rh. bengalensis* Timm, 1956.

Bresslau and Schuurmans Stekhoven, in Schuurmans Stekhoven (1935) described a new species, *Rh. velata,* from Heligoland. The description was based on one male and one female, the male apparently differing from *Rh. marina* particularly in the form of the spicules and the shape of the tail. We have seen one male specimen which on first examination appeared to belong to, and was initially referred to this species, but a more careful study showed it to be a poorly preserved specimen of *Rh. marina*, or a late fourth-stage larva, in which the caudal alae appeared to be more extensive than usual and in which the form of the spicules could only be established with difficulty. The appearance of the specimen is so very similar to the figure given by Bresslau and Schuurmans Stekhoven for *Rh. velata* that we have no hesitation in referring that name to the synonymy of *Rh. marina*.

Rhabditis fluviatilis Bütschli, 1876 was redescribed by Hirschmann (1952) ; Osche (1954) then drew attention to the great similarity between it and *Rh. marina* but said that he was unable to decide whether or not they were indistinguishable since his specimens of *Rh. marina* were in such a poor condition that he was unable to determine the form of the amphids or to establish the presence of lateral fields. Meyl (1955), however, considered *Rh. fluviatilis*, from Magdeburg, to be indistinguishable from *Rh. marina* var *septentrionalis*, also reporting *Rh. m.* var. *marina* from the same area. We are able to confirm the validity of this synonymization since our specimens agree in all particulars with the descriptions given by both Büstchli and Hirschmann. Further evidence in support of this conclusion, and also our refusal to accept two subspecies, is given by Andrássy (1958) who figures the range of variation in the shape of the female tail in *Rh. fluviatilis* (see Andrássy, 1958. Text-fig. 11, C–E).

The records of *Rh. marina* show it to be widespread on the coasts of Europe and the Mediterranean (see records from the coast of Algeria in Gerlach, 1954*b*). It also appears probable that it is common on the Atlantic coasts of both North and South America but there are no wholly reliable records of it occurring anywhere else, although it may later be shown to be cosmopolitan. The records from " non-marine " localities, all of which are European, generally refer to it as a rare species from habitats characterized by extreme decomposition (Hirschmann, 1952 and, probably, Bütschli, 1876). Hirschmann records it at Regnitz and Pegnitz, Bavaria from " Wasser . . . trüb und stinkend . . . " while Meyl (1955) reports it, also as a rare species, from several localities of fairly high salinity (Salzbiotopen) near Magdeburg and Andrássy (1958) reports it from Hungary as a rare species in heavily manured soil.

As Osche (1954) has pointed out, many of the records of so called marine species of *Rhabditis* clearly represent species which have been swept into such localities by accident and cannot be considered true marine forms. The position with *Rh. marina* seems to be slightly different but we would still consider it a terrestrial saprophagous form which is able to survive under conditions of fairly high salinity. Many of the records of this species refer to specimens found in association with sea-weeds in the littoral zone, but in most cases very few specimens have been found. On the other hand Ditlevsen (1912) obtained relatively large numbers of specimens from putrefying sea-weed and we also found large numbers under similar conditions. It appears that *Rh. marina* is characteristic of such conditions of fairly extreme decomposition and it is clear that the specimens found in the littoral zones have been swept there by accident and almost certainly cannot live and reproduce under such conditions. Nevertheless *Rh. marina* is unusual in being the species of *Rhabditis* most commonly found on beaches so that it can be considered to represent a form which is adapted to living under semi-marine conditions and must be treated as a typical member of the beach fauna.

Rhabditis (Pellioditis) ehrenbaumi Bresslau and Schuurmans Stekhoven, 1935

Synonymy :

Rhabditis ehrenbaumi Breslau & Schuurmans Stekhoven, in Schuurmans Stekhoven, 1935. *Tierw. N. -u. Ostsee* **5** (b) : 155. Figs. 3392–*c* ; Bresslau & Schuurmans Stekhoven, 1940. *Marine Freilebende Nematoda aus der Nordsee*, Bruxelles, p. 70. Taf. XIV, Abb. 80–81.
Rhabditis (*Choriorhabditis*) *ehrenbaumi*, Osche, *Zool. Jb.* (Syst. etc.) **81** : 263.
Rhabditis (*Pellioditis*) *ehrenbaumi*, Dougherty, 1955. *J. Helminth.* **29** : 131.

Type locality : among *Ceramium rubrum*, Heligoland (no more precise locality given).

Material studied

5 ♂, 8 ♀. (B.M. (N.H.) Reg. Nos. 1960.32–41) from among rotting sea-weed and other plant matter cast up on beach, just above high water mark, at Neyland, Pembrokeshire, South Wales (August, 1959).

6 ♂, 6 ♀, 3 4th-stage larvae. (B.M. (N.H.) Reg. Nos. 1960.1213–1227) from among very rotten and strong smelling sea-weed and other plant matter on beach at bottom of cliff path, Jennicliffe Bay, Plymouth (July, 1960).

A few specimens were also found in rotting sea-weed mixed with other plant matter, high on the beach at Weston-Super-Mare, Somerset. *Rh. marina* was also present (see record above), (November, 1960).

Measurements : (specimens fixed in cold formalin and mounted in glycerine).

From Neyland
Males (5)

Body length (mm.)	*a*	*b*	*c*	V
0·89	17·0	4·1	32·0	—
0·96	13·8	3·4	27·4	—
1·05	16·8	3·2	25·3	—
1·28	17·0	4·1	32·0	—
1·28	18·3	3·9	32·0	—

Females (8)

1·01–1·45 (1·271±0·145)	14·2–18·2 (16·08±1·45)	3·6–4·6 (4·01±0·118)	17·5–22·7 (20·09±1·382)	53–60 (56·1±2·21)

From Jennicliffe Bay
Males (6)

Body length (mm.)	*a*	*b*	*c*	V
1·33	16·6	4·0	33·3	—
1·34	16·7	4·2	33·5	—
1·47	21·0	3·8	49·0	—
1·51	18·9	4·3	37·7	—
1·60	17·8	4·7	53·3	—
1·64	20·5	4·3	41·0	—
Females (6)				
1·38	15·3	3·6	19·7	52·9
1·49	14·9	4·0	24·8	52·3
1·56	19·5	4·2	22·3	55·8
1·62	20·3	4·1	18·0	53·7
1·62	20·3	4·2	20·3	54·3
1·64	18·2	3·9	18·2	56·7
Larvae				
0·75	15·0	3·4	9·4	—
0·89	22·2	3·4	11·1	—
0·97	19·4	3·6	9·7	—

MORPHOLOGY

General

The body is relatively stout and terminates posteriorly in a very short tail in both sexes. The specimens are in rather poor condition; they were killed and fixed in cold formalin. There are no lateral fields but there appear to be distinct narrow lateral alae running almost the full length of the body in both sexes. The oesophagus is typical with the anterior part roughly the same width as the posterior isthmus. The valves in the posterior bulb are marked with concentric semi-elliptical ridges as in *Rh. marina* and the metastome bears five tubercles.

Head

The head is very similar to that of *Rh. marina* and the distribution of the cephalic papillae seems to be the same, except that we have been unable to find any indication of an inner circle of papillae. Although the outer two pairs of papillae are slightly setiform, those of the inner circle appear to be wholly sessile. The amphids are relatively prominent and the structure of the lip-lobes and the underlying lining of the buccal cavity is identical with that of *Rh. marina* (Text-fig. 2*c*).

Male

The tail is short and broad, with very narrow caudal alae beyond which the terminal spike of the tail does not project. There are ten pairs of narrow papillae, or rays, supporting the alae, of which the most anterior pair lies alone, slightly anterior to the cloacal opening. followed by a group of seven pairs which are all roughly the same size except for those making up the second pair from the posterior end which are distinctly longer and narrower than the others. The phasmids open on the ventral surface of the tail just anterior to the long pair of papillae (Text-fig. 2*h*). The spicules are equal in length, identical in structure and are not fused. They terminate posteriorly in simple sharp points and bear rather broad double alae. The gubernaculum is about one third the length of the spicules and widens anteriorly. There is a single testis which is reflexed and which does not appear to have any ejaculatory glands (Text-fig. 1*c*).

Female

The reproductive apparatus is amphidelphic and didelphic with oviducts modified as spermathecae as in *Rh. marina*. The eggs are relatively large and are spherical in shape, about 0·035–0·045 mm. × 0·070–0·095 mm. in size. The greatest number seen in the uteri at one time is six (Text-fig. 1*b*). The tail is short and very stout with a fine evenly narrowing terminal spike (Text-fig. 2*k* and Text-fig. 4). The phasmids open just anteriorly to the commencement of the terminal spike. The vulva opens slightly posteriorly to the middle of the body, V = 52–68.

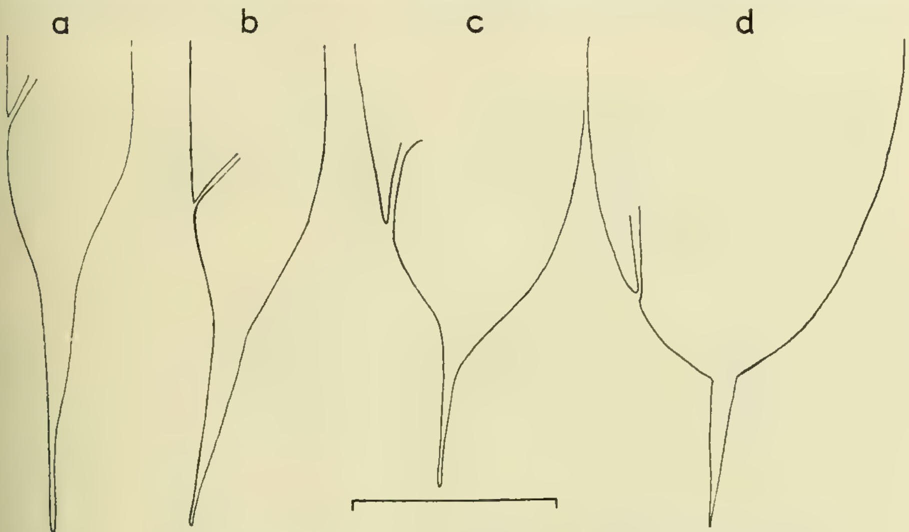


FIG. 4. *Rhabditis ehrenbaumi*, outline of tail: *a* and *b*, larvae; *c* and *d*, adults. (Scale line = 0·05 mm.)

Larva

The fourth-stage larva is very similar to the adults, the only marked difference, other than those shown by the reproductive organs, is in the shape and proportions of the tail. In the larvae it is much less stout, is relatively longer and tapers more evenly than in the adult (Text-fig. 4). This is shown most clearly by the low value of " c " (body length/tail length) in the larvae compared with the adults.

Discussion

This species, like *Rh. marina*, appears to be a terrestrial saprophagous form whose presence among *Ceramium rubrum* at Heligoland was accidental, since the decomposing matter among which we found it, although largely composed of sea-weed. contained straw and other rotting terrestrial plant remains at all localities, Further, the habitats at the localities in which it was found were relatively much higher up the beach than those from which *Rh. marina* alone was obtained and it is doubtful if this species may even be considered a typical member of the beach fauna as *Rh. marina* certainly can be. The whole question cannot be resolved at this time as our records are the first reports of this species since the original description.

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BY

G. PALMER

Department of Zoology, Brit. Mus. (Nat. Hist.)

Pp. 335–351 (*with Pl.* 62; 1 *Text-fig.*)

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(With 3 Text-figs.)

SUMMARY

1. The species of *Trachipterus* occurring in the Mediterranean and north-east Atlantic are reviewed.

2. *Trachipterus cristatus* is considered to be generically distinct and is placed in a separate genus.

3. *Trachipterus gryphurus* Lowe is regarded as a synonym of *T. arcticus* and *T. pentastigma* Norman as a synonym of *T. trachypterus*.

4. Comments are made on the young stages, sexual dimorphism and food of Trachipterids.

5. A brief description of the swim bladder is given.

INTRODUCTION

THE systematics of the fishes of the genus *Trachipterus* (s.l.) are in a somewhat confused state, the main reason for this being that these fishes are comparatively rare in museum collections. Their fragility is such that few unmutilated examples have been available for study, and many of the nominal species have been described from single specimens. Furthermore, it is known that allometric growth occurs at certain stages, the extent of which has not been fully investigated.

The present paper has resulted from the difficulty experienced in identifying a juvenile example from the Orkneys.*

The Dealfishes are widely distributed and are known to occur in the Arctic, Atlantic, Indo-Pacific and Mediterranean regions. Some thirty nominal species have been described, but the work I have done on this family suggests that there may be comparatively few species, each having a fairly wide geographical range.

In 1861 Günther listed nine species of *Trachipterus*, eight of which were said to occur in the Mediterranean and north east Atlantic. Since that time an additional fifteen species have been described from various localities, including two from the area under consideration, these latter being *T. filicauda* Costa (1862) and *T. gavardi* Bounhiol (1923).

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* For a comprehensive study of the order Allotriognathi, reference should be made to a series of papers to be published by Walters and others.

In his work on the young stages of *T. taenia*, Emery (1878–79) was able to demonstrate for the first time the changes that take place in these fishes during successive growth stages and on the basis of this work came to the conclusion that *T. filicauda*, *T. spinolae*, *T. taenia* and *T. trachypterus* were synonymous, being different growth stages of the same form.

Lütken (1881) reduced still further the number of species and to-day it is generally accepted that only three taxons should be recognized from the Mediterranean and NE. Atlantic areas. These are *T. arcticus*, a northern form, and *T. trachypterus* and *T. cristatus*, both more southerly species. *T. cristatus* differs so markedly from the other two species that it warrants generic status. Walters and Fitch (1960) have reached the same conclusion and I shall consequently be using their name in preference to that which I was proposing to use.

The only other species which has been recorded from the North Atlantic is *T. trachyurus*, described by Poey (1856–58). This is known only from the type, taken off Cuba, and one other specimen taken off Florida in 1952, and appears to be confined to the western North Atlantic. This species is quite distinct from both *T. arcticus* and *T. trachypterus*, differing in the lower dorsal ray count (82) and in the form of the gill-rakers, which in *T. trachyurus* lack the fringe of bristle-like setae found in the other species.

In the past, the keys which have been provided for the distinction of the species have been based largely on descriptions and not on an examination of actual specimens. As an example, Goode and Bean (1896) ignored the work of Emery and Lütken and gave a key to a number of species, which had been adapted from an earlier work by Moreau (1881). More recently, Lozano y Rey (1947) and Smith (1949) have given keys for the three forms currently recognized from this area.

As the species of the genus *Trachipterus* (s.l.) here considered are now placed in two genera, the following key for their separation has been included.

KEY TO THE MEDITERRANEAN AND N.E. ATLANTIC GENERA

1. Body scaleless; ventral profile not constricted behind vent. Lower rays of caudal fin reduced to stumps in adults. Vertebrae 84 to 102. No bulbous flaps on fin-rays at any stage. Colour pattern uniform silvery or brown, with usually 1 to 5 large dark blotches along sides of body . . . . *Trachipterus*
2. Deciduous cycloid scales present on body. Ventral profile crenulate and sharply constricted behind the vent. Lower caudal rays not so reduced as in *Trachipterus*. Vertebrae 62 to 69. Bulbous flaps present on dorsal and pelvic rays in young stages. A number of dark transverse markings along the trunk and caudal regions *Zu*

Trachipterus Gouan

Trachipterus Gouan, 1770. *Hist. Pisc.*: 104 and 153 (*Cepola trachyptera* Gmelin).
Gymnogaster Brünnich, 1788. *K. Dansk. vid Selsk.* **3**: 408 (*arcticus*).
Trachypterus Schneider, 1801. *Blochii Syst. Ichth.*: 480 (*taenia*).
Bogmarus Schneider, 1801. *Blochii Syst. Ichth.*: 518 (*islandicus*).
Argyctius Rafinesque, 1810. *Caratt. nuov. Gen.*: 55 (*quadrimaculatus*).
Cephalepis Rafinesque, 1810. *Ind. Ittiol. Siciliana*: 54 (*octomaculatus*).
Epidesmus Ranzani, 1818. *Opusc. Sci. Bologna*: 137 (*maculatus*).

Body elongate, compressed, scaleless ; dorsal and ventral outlines tapering more or less evenly from head to caudal fin. Recurved, pointed teeth in both jaws, 6 to 12 in the upper, 6 to 10 in the lower. Vomer with 1 to 2 median teeth. Palatine teeth, if present, feeble. Nostrils single. One dorsal fin, consisting of 145 to 190 rays, the first 5 or 6 elongate, at least in the young. Pectorals of 9 to 12 rays. Pelvics 3 to 9, long and filamentous in young stages but reduced to stumps in adults. No anal fin. Caudal fin in two parts ; the upper lobe of 6 to 10 well developed rays, often set at right angles to the longitudinal axis of the body ; the lower lobe of 2 to 7 rudimentary rays in adults. Lateral line straight, running the length of the body, armed with small forwardly directed spines which become larger posteriorly. Gill rakers on first arch 3 to 4 + 7 to 10. Branchiostegal rays 6. Vertebrae 84 to 102. Swim bladder present, much reduced in adults.

Key to Mediterranean and N.E. Atlantic Species

1. Greatest depth of body ¼ to ⅓ of the way along its length, except in specimens of less than 300 mm. ; depth of caudal peduncle contained more than twice in depth of body at 10th lateral line spine forward from the caudal fin. Body axis approximately a straight line in adults (see Pl. 62, fig. 1) . . . . . . *arcticus*
2. Greatest depth of body immediately behind head ; depth of caudal peduncle contained less than twice in depth of body at 10th lateral line spine forward from caudal fin. Body axis upcurved in the posterior caudal region in adults (see Pl. 62, fig. 2) *trachypterus*

Trachipterus arcticus (Brünnich)

Trichiurus lepturus Mohr, 1786 (nec Linnaeus). *Forsøg til en Islandsk Naturhist.* Copenhagen : 63 (Iceland) ; Pálsson, 1791–97 (1945). *J. Naturf. Reise Island* : 36 and 187 (Iceland) (fide Saemundsson, 1949) ; Hoy, 1815. *Trans. Linn. Soc. Lond.* **11** : 210 (Moray Firth).

Gymnogaster arcticus Brünnich, 1788. *K. Dansk. Selsskr. N. Saml.* **3** : 408 tab. B, figs. 1–3 (Iceland) ; Faber, 1829. *Naturg. Fische Islands* : 66 (general) ; Cuvier, 1829. *Règn. Anim. Ed.* **2** : 219 (description) ; Fleming, 1831. *Ann. Mag. nat. Hist.* **4** : 215, fig. 34 (Orkneys); Nilsson, 1832. *Prod. Ichth. Scand.* : 107 (synonymy, distribution) ; Jenyns, 1835. *Brit. Vert.* : 372 (synonymy, description) ; Swainson, 1839. *Nat. Hist. Fishes, Amphib., Rept.* **2** : 258 (generic diagnoses) ; Duduid, 1851. *Proc. zool. Soc. Lond.* : 116 (Orkneys).

Bogmarus islandicus Schneider, 1801. *Blochii Syst. Ichth.* **2** : 518, pl. 101 (Iceland).

Trachypterus arcticus, Nilsson, 1855. *Skand. Faun. Fisk.* **4** : 162 (Scandinavia) ; Günther, 1861. *Cat. Fish. Brit. Mus.* **3** : 305–306 (synonymy, description) ; Collett, 1875. *Norges Fiske, Christiania* : 78 (Norway) ; Newman, 1875. *Zoologist* (2) **10** : 434 (Donegal Bay) ; Edwards, 1879. *Zoologist* (3) **3** : 220 (Banffshire coast) ; Day, 1880–84. *Fishes of Great Britain and Ireland* **1** : 217, pl. 63 (synonymy, description) ; Lütken, 1882. *Vid. Selsk. Forh.* : 206–216 (synonymy) (translated in *Ann. Mag. nat. Hist.* (5) **11** : 176–184, 1883) ; Schneider, 1882. *Vid. Selsk. Forh.* No. 15 : 1–6 fig. (Scandinavia) ; Collett, 1885. *Norges Fiske, Christiania* (2nd suppl.) : 69 (Norway) ; Meek, 1890. *Stud. Dundee Mus.* **1**, No. 6 : 1–24, 2 pls., 9 figs. (anatomy) ; Lilljeborg, 1891. *Sver. Norges Fiskar. Uppsala* **1** : 462 (synonymy, description) ; Smitt, 1893. *Scandinavian Fishes* **1** : 315, fig. (general) ; Goode and Bean, 1895. *Oceanic Ichth.* : 479, fig. (synonymy) ; Traquair, 1896. *Ann. Scot. nat. Hist.* : 159 (Shetland Isl.) ; Cursiter, 1896. *Ann. Scot. nat. Hist.* : 160 (Orkneys) ; Clarke, 1900. *Ann. Scot. nat. Hist.* : 13 (Firth of Forth) ; Collett, 1902–05. *Norges Fiske, Christiania* (3rd suppl.), No. 1 : 99 (Norway) ; Lemmon, 1905. *Ann. Scot. nat. Hist.* :184 (Banffshire coast); Evans, 1909. *Ann. Scot. nat. Hist.*: 20 (Scottish coast); Cole, 1913. *Nature*, **91**: 607 (Grimsby Mkt); Thompson, 1918. *Scot. Nat.*: 67–68 (Rockall and St. Kilda); Wolleback, 1924. *Norges Fiske, Christiania*: 218 (distribution); ? Barnard, 1925. *Ann. S. Afr. Mus.* **21**, Pt. 1: 353, fig. (doubtful S. African record); Saemundsson, 1926. *Fiskarnir, Reykjavik*: 155 (Iceland); Matheson, 1930. *Ann. Mag. nat. Hist.* (10) **6**: 683–685 (west of Ireland); Buen, 1935. *Inst. esp. Oceanogr. Not. y Res.* (2) No. 88: 78 (Atlantic); Nobre, 1935. *Peixes de Portugal*, **1**: 162, fig. (Portugal); Ehrenbaum, 1936. *Naturg. Wirtsch. Bedeutung Seefische Nord-Europas, Stuttgart*: 153, fig. 129 (description, distribution); Lozano y Rey, 1947. *Fauna Iberica, Peces*, **2**: 693, fig. (key to species); Smith, 1949. *Sea Fishes of S. Africa*: 142 (S. African record and key to species); Went, 1952. *Irish Nat. J.* **10**: 302 (Ireland); Andryashev, 1954. *Tabl. anal. Faune URSS No.* 53: 207, fig. (description, distribution).

Trachypterus bogmarus Cuv. and Val., 1835. *Hist. nat. Poissons*, **10**: 346 (synonymy, Norway); Reinhardt, 1835–1836 (1837). *K. dansk. vid. Selsk.*: 3 (Faroe Isl.); Bonaparte, 1846. *Cat. met. Pesci Europei*: 79 (synonymy).

Gymnetrus arcticus, Yarrell, 1836. *Brit. Fishes*, **1**: 191 (description).

Trachypterus vogmarus Reinhardt, 1838. *K. dansk. vid Selsk.* **7**: 67 (Denmark); Hallgrimsson, *c.* 1845 (1936). *Islenzk Dyr*, **3**, Pt. 3–5: 98 (*fide* Saemundsson, 1949); Gröndal, 1891. *Pisces Islandiae*: 46 (*fide* Saemundsson, 1949).

Vogmarus islandicus, Reid, 1849. *Ann. Mag. nat. Hist.* (2) **3**: 456 (Scotland).

Trachypterus gryphurus Lowe, 1850. *Proc. Zool. Soc. Lond.*: 248 (Madeira); Günther, 1861. *Cat. Fish. Brit. Mus.* **3**: 301 (description); Goode and Bean, 1895. *Oceanic Ichth.*: 478 (description).

Trachypterus iris Priol. (nec Walbaum), 1944. *Rev. Trav. Off. Pêche marit.* **13**: 432, fig. (from *Germo* stomach, off coast of Spain).

D. 150–190; A. 0; V. 5–6; P. 9–11; C. 8 + 5–6. Branchiostegal rays 6. Vertebrae 99 to 102.

Body strongly compressed, greatest depth about midway between occiput and vent in adults, from which point the body tapers more or less evenly dorsally and ventrally to the caudal fin. Ventral profile conspicuously armed with wart-like tubercles, especially in large specimens. Anterior profile of head straight, sharply declivous in young when mouth is retracted. Eye of moderate size. Teeth in upper jaw slender, almost horizontal, their distal ends pointing backwards. Usually 6 to 12 in number. Those in the lower jaw stronger, slightly recurved, 6 to 9 in number. Three to 5 teeth on the vomer, none on the palatines. Gill rakers on first arch 3 to 4 + 7 to 10. A single dorsal fin, the first 5 or 6 rays greatly prolonged in young stages, but never with bulbous flaps. Pelvics extremely elongate in young stages, but vestigial in adults. Caudal fin in two parts, the upper lobe of 8 well developed rays, the lower lobe of 5 or 6 rudimentary rays. The upper lobe of this fin is usually set at right angles to the body axis in adults. Scales absent, except for a modified series along the lateral line, each of which is armed with a small forwardly directed spine. These spines increase in size towards the posterior end of the body. Scattered over the body are numerous small pit-like depressions, the structure and function of which have not been studied. Stüwitz (1840) figures both the lateral line scales and the pit-like depressions.

Eighteen specimens have been examined, ranging in length from 32 to 1,630 mm. The largest specimen to have been recorded in recent years is one of 2,515 mm. length, trawled near the Porcupine Bank off the west coast of Ireland.

Colour: Silvery, with usually from 1 to 5 dark spots along the body. These may completely disappear in large examples and the overall body colour become brownish. In life, the dorsal fin is red.

I have examined Lowe's unique example of *T. gryphurus* described by him in 1850 from Madeira. Although in a poor state of preservation, this specimen appears to be conspecific with examples of *T. arcticus*. The accompanying table indicates that *T. gryphurus* agrees more closely with *T. arcticus* than with *T. trachypterus*.

	gryphurus	*arcticus*	*trachypterus*
Average number of dorsal rays	170 (1)	169·5 (18)	164·8 (44)
,, ,, ,, vertebrae	100 (1)	99 (18)	90 (44)
Depth of caudal peduncle into depth of body at 10th lateral line spine forward from caudal	2·5 (1)	2·2–5 (18)	1·3–2 (44)

The number of specimens of each species examined is indicated in brackets.

The type of *T. gryphurus* is here figured for the first time.

In younger stages of *T. arcticus* (i.e. specimens below 300 mm. in length) the greatest depth of the body is immediately behind the head as in *T. trachypterus*, but whereas in *T. arcticus* this depth remains more or less constant to about ⅓ of the way along the body length before the gradual tapering to the caudal begins, in young examples of *T. trachypterus* this tapering commences immediately behind the occiput.

T. arcticus is a north-eastern Atlantic species which does not seem to occur in the western North Atlantic. It has not been possible to ascertain satisfactorily its southerly limits from existing records, but it has not been reported from the Mediterranean.* There is one record from Madeiran waters and Priol (1944) figures and describes ten juvenile examples of what he calls *T. iris* from the stomach of an albacore (*Germo alalunga*), which was captured north west of Finisterre. From the information given, however, it is clear that these fishes are examples of *T. arcticus.*

The breeding areas of this species do not appear to be known, but it is probable that spawning occurs at considerable depths in off-shore waters. Andryashev (1954) states that shoals of several hundreds of these fishes may be observed off the north-east coast of Iceland, varying in length from 900 to 2,060 mm. Unfortunately, no indication is given as to whether or not this is a seasonal occurrence. In this connection, it is of interest to note the comparatively large influx of this species into Scottish waters in the year 1954 when fifteen specimens were recorded, none being less than 830 mm. in length.

It has been reported on a number of occasions by Scandinavian fishermen that they have seen these fishes floating on their sides at or near the surface. A more recent report of a similar occurrence has been made by Mr. S. Willis. In November,

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* Since this paper went to press, I have seen a report by Planas and Vives (1956) which records the occurrence in the Mediterranean of three specimens of *T. arcticus*, 425–529 mm. in length.

1955, some 200 miles west of Lands End, he saw seven or eight objects of varying size floating on the surface. Closer inspection showed that they were fishes and from his description they were almost certainly examples of *T. arcticus*. He states that they were floating on their sides, moving feebly as though stunned. The reason for this behaviour is not apparent, but may be abnormal.

A juvenile example of this species has recently been received from Dr. J. H. Fraser of Aberdeen. It was taken off the west coast of Ireland (54° 10′ N., 12° 10′ W.) in an oblique haul from 250 to 0 metres. A brief description of the specimen is given below.

It is 32 mm. in standard length and appears to be one of the smallest examples of this species reported on. At this stage it is apparent that ossification of the finrays is not yet completed as the dorsal count is considerably lower than the mean for an adult of this species. Similarly, only eight pectoral rays are at present ossified. Caudad to the last stained dorsal ray and continuous with it is a lobe containing a number of thin filamentous structures, which may be actinotrichia. There is also a similar structure on the ventral surface, which is not present in the adult. The vertebral count of 99, of which 45 are pre-caudal, places this specimen as an example of *T. arcticus*. At this stage all the vertebrae are of approximately the same length. The caudal fin consists of eight rays in the upper lobe and six on the ventral lobe. The rays in this lower lobe are well developed in this specimen, although in the adult they become obsolescent, as is the case with the pelvic rays. The pectorals have eight ossified rays plus three or four which are still unossified.

Measurements and counts for this specimen are as follows:

Standard length: 32 mm.

D: 143 + unossified rays. The first five rays are elongate.

A: 0.

Pectorals: 8 + 3 or 4 which are not yet ossified.

Pelvics: 8.

Caudal: 8 + 6.

Vertebrae: 99 (of which 45 are pre-caudal).

Greatest depth, which is immediately behind the occiput, 4 in the length.

DISTRIBUTION. Eastern North Atlantic from Iceland to Madeira and into the North Sea.

Trachipterus trachypterus (Gmelin)

Cepola trachyptera Gmelin, 1788. *Syst. Nat.* **1**, Pt. 3 : 1187 (Adriatic).
Cepola iris Walbaum, 1792. *Artedi Bibl. Philos. Ichth.* **3** : 617.
Trachypterus taenia Schneider, 1801. *Blochii Syst. Ichth.* **2** : 480 (Adriatic) ; Bonaparte, 1846. *Cat. met. Pesci Europei No.* 711 : 78 (synonymy) ; Costa, 1850. *Faun. règn. Napoli*, **2** : 3, pl. ix ; Erhard, 1858. *Faun. der Cycladen, Leipzig* : 89 (Greek waters) ; Günther, 1861. *Cat. Fish. Brit. Mus.* **3** : 302 (description) ; Canestrini, 1872. *Fauna d'Italia*, Pt. 3 : 193 (description) ; Heldreich, 1878. *La faune de Grèce, Athens* : 87 (Greek waters) ; Emery, 1879. *Mem. Atti R. Accad. Lincei*, **3** : 390 (growth stages) ; Emery, 1879. *Mitt. zool. Sta.*

Naples, **1** : 581 (growth stages) ; Giglioli, 1880. *Elenco dei Mammiferi, etc.* : 92 (Nice and Elba) ; Gogorza, 1883. *Ann. Soc. esp. Hist. nat.* **12** : 75, 78 (Mediterranean) ; Apostolides, 1883. *La pêche en Grèce, Athens* : 11, 23 (Greece) ; Carus, 1889. *Prod. Faun. medit.* : 699 (description and distribution) ; Apostolides, 1907. *La pêche en Grèce* (2nd Ed.) : 8, 16 (Greece) ; Fage, 1907. *Arch. zool. exp. gen.* (4) **7** : 73 (listed from Balearic Isl.) ; Lo Bianco, 1908–1909. *Mitt. zool. Sta. Naples,* **19** : 1, figs. (eggs and larvae) ; Jacino, 1909. *Arch. zool. Naples,* **3,** Fasc. 4 : 479 (eggs and larvae) ; Kaschkaroff, 1913. *Anat. Anz.* **44** : 214 (structure of epidermis) ; Devedjian, 1926. *Pêches et pêcheries en Turquie* : 144, fig. (Turkish coast) ; Bertin, 1929. *Bull. Soc. zool. Fr.* **54** : 164 (description) ; Sparta, 1931. *Fauna e flora del Golfo di Napoli,* **38** : 267 (young stages) ; Dieuzeide and Goeau-Brissoniere, 1940. *Bull. Sta. Aquic. Pêche, Castiglione* (N.S.), No. 1 : 81, figs. (Algeria) ; Dieuzeide, Novella and Roland, 1954. *Bull. Sta. Aquic. Pêche, Castiglione* (N.S.), No. 5 : 146, figs. (description, distribution).

Gymnetrus cepedianus Risso, 1810. *Ichth. Nice, Paris* : 146, fig. (Mediterranean) ; Risso, 1826. *Hist. nat. Europ. mérid.* **3** : 295 (description).

Argyctius quadrimaculatus Rafinesque, 1810. *Caratt. alcun. nuov. Gen. Siciliana* : 55 (Sicily).

Cephalepis octomaculatus Rafinesque, 1810. *Indice ittiol. Siciliana* : 55 (Messina) ; Swainson, 1839. *Fishes, Amphib. Rept.* **2** : 404 (description)

Epidesmus maculatus Ranzani, 1818. *Opusc. Sci. Bologna,* **2** : 133, pl. 6 (Adriatic).

B(r)ogmarus aristotelis Risso, 1820. *J. Phys. Chim. Hist. nat. Paris,* **91** : 249 (Nice).

Bogmarus mediterraneus Otto, 1821. *Conspic. Anim.* : 6 (Mediterranean).

Regalecus maculatus, Nardo, 1824. *Giorn. Fisica, Pavie,* **8** : 116 (not seen ; fide Costa, *Faune Règne Napoli*).

Trichiurus trimaculatus Giovene, 1829. *Mem. Soc. ital.* **20**, Pt. 1 : 25 (Mediterranean).

Trachypterus spinolae Cuvier and Valenciennes, 1835. *Hist. nat. Poissons,* **10** : 328 (Nice) ; Bonaparte, 1846. *Cat. met. Pesci Europei,* No. 712 : 79 (synonymy ; Mediterranean) ; Canestrini, 1861. *Arch. Zool. Anat. Fis. Genova,* **1,** Fasc. 1 : 26 (Gulf of Genoa) ; Günther, 1861. *Cat. Fish. Brit. Mus.* **3** : 300 (description and distribution) ; Canestrini, 1872. *Fauna d'Italia,* Pt. 3 : 193 (Naples, Sicily) ; Giglioli, 1880. *Elenco dei Mammiferi, etc.* : 91 (Nice, Elba, Naples) ; Moreau, 1881. *Hist. nat. Poissons,* **2** : 565, fig. (description and synonymy) ; Bertin, 1946. *Petit Atlas des Poissons,* **1** : 81, fig. (brief diagnosis).

Trachypterus falx Cuvier and Valenciennes, 1835. *Hist. nat. Poissons,* **10** : 333 (Spain) ; Moreau, 1881. *Hist. nat. Poissons,* **2** : 558 (description and synonymy) ; Fage, 1907. *Arch. Zool. exp. gén.* (4) **7** : 73 (listed from Balearic Islands).

Trachypterus iris, Cuvier and Valenciennes, 1835. *Hist. nat. Poissons,* **10** : 341, pl. (Adriatic) ; Günther, 1861. *Cat. Fish. Brit. Mus.* **3** : 303 (description, distribution) ; Canestrini, 1861. *Arch. Zool Anat. Fis. Genova,* **1,** Fasc. 1 : 262 (Gulf of Genoa) ; Carruccio, 1870. *Cat. degli Anim. Sicilia* : 32 (Cagliari) ; Emery, 1879. *Zool. Sta. Napoli,* **1** : 581 (young stages) ; Giglioli, 1880. *Elenco dei Mammiferi, etc.* : 92 (Livorno, Elba and Cagliari) ; Moreau, 1881. *Hist. nat. Poissons,* **2** : 561 (description, synonymy) ; Goode and Bean, 1895. *Oceanic Ichth.* : 477, fig. (description, synonymy) ; Damiani, 1896. *Riv. ital. Sci. nat. Siena,* **16** : 132 (Genoa) ; Parona, 1898. *Atti Soc. Ligust. Sci. Genova,* **9** : 350 (Ligurian Sea) ; Barnard, 1925. *Ann. S. Afr. Mus.,* **21** : 353 (S. Africa) ; Buen, F. de, 1926. *Res. Camp. Inst. esp. Oceanogr.* No. 2 : 72 (Catalan Sea, Balearic Isl.) ; Mourgue, 1931. *Bull. Soc. Linn. Lyon,* **10** : 39 (abundance in Mediterranean) ; Kamohara, 1934. *Zool. Mag. Tokyo,* **46** : 462, fig. (Japan) ; Buen, F. de, *Inst. esp. Oceanogr. Not. y Res.* (2), No. 88 : 78 (Mediterranean) ; Ninni, 1939. *Atti Soc. ital. Milan,* **78** : 224 (synonymy) ; Matsubara, 1941. *Suisan Kenkiushi Japan,* **36,** No. 2 : 34 (Japan) ; Lozano y Rey, *Fauna Iberica Peces,* **2** : 686, figs. (description, synonymy) ; ? Barnard, 1947. *A pictorial guide to S. African fishes, Cape Town* : 84, pl. X, fig. 2 (Table Bay ; the figure is that of *T. arcticus*) ; King and Ikehara, 1956. *Pac. Sci.* **10** : 22–23 (Central Pacific).

Trachypterus leiopterus Cuvier and Valenciennes, 1835. *Hist. nat. Poissons,* **10** : 342 (Naples and Nice) ; Günther, 1861. *Cat. Fish. Brit. Mus.* **3** : 304 (description, distribution) ; Giglioli, 1880. *Elenco dei Mammiferi, etc.* : 92 (Nice, Genoa, Messina) ; Moreau, 1881.

Hist. nat. Poissons, **2** : 563 (description, synonymy) ; Carus, 1889–1893. *Prod. Faun. Médit.* : 700 (description, distribution) ; Goode and Bean, 1895. *Oceanic Ichth.* : 479 (general notes) ; Damiani, 1896. *Riv. ital. Sci. nat. Siena*, **16** : 132 (Genoa) ; Parona, 1898. *Atti Soc. Ligust. Sci. Genova*, **9** : 350 (Ligurian Sea) ; Tortonese and Trotti, 1950. *Atti Acad. Ligure*, **6** : 99 (Ligurian Sea).

Trachypterus costae Cocco, 1838. *Giorn. Il Faro*, **4**, Anno 6 : 4, figs. 1a and b. (Messina).

Cephalepis swainsonii Rafinesque in Swainson, 1839. *Fishes, Amphib. Rept.* **2** : 404 (Sicily).

Trachypterus rondeletii Costa, 1850. *Fauna Regn. Napoli*, **2** : 10, fig. IX bis (Naples).

Trachypterus rüppellii Günther, 1861. *Cat. Fish. Brit. Mus.* **3** : 304 (Mediterranean) ; Carus, 1889–93. *Prod. Faun. Médit.* : 700 (description) ; Goode and Bean, 1895. *Oceanic Ichth.* : 479 (references copied).

Trachypterus trachypterus, Hamilton, 1916. *Trans. Proc. N.Z. Inst.* **48** : 374, figs. (review of New Zealand species) ; Pietschmann, 1925. *Veroff. naturhist. Mus. Wien*, **5** : 6, figs. (popular account) ; Phillipps, 1927. *Fish. Bull. Wellington, N.Z.*, No. 1 : 26 (listed from New Zealand) ; Fowler, 1936. *Bull. Amer. Mus. nat. Hist.* **70** : 492 (description) ; Tortonese, 1948. *Bol. Pesca Piscic. Idrobiol.* **23** (N.S.) **2** : 19 (Aegean Sea) ; Tortonese and Trotti, 1950. *Atti Accad. Ligure*, **6** : 99 (Ligurian Sea) ; Tortonese, 1952. *Natura, Milan*, **43** : 28 (Ligurian Sea).

Trachypterus pentastigma Norman, 1922. *Ann. Mag. nat. Hist.* (9) **10** : 217 (Japan) ; Matsubara, 1941. *Suisan Kenkui-shi*, **36**, No. 2 : 34 (affinities).

Trachypterus arcticus, Barnard (nec Brünnich), 1948. *Ann. S. Afr. Mus.* **36** : 359, fig. (S. Africa).

D. 145–185; A. 0; V. 5; P. 9–11; C. 8 + 5 rudiments; branchiostegal, rays 6; Vertebrae, 84–96.

This species occurs in large numbers in the Mediterranean, which appears to be one of its main spawning areas. Eggs and larvae, as well as adults, have been recorded from this sea on many occasions. It has also been recorded from Japan (Norman, 1922 ; Kamohara, 1934 and Matsubara, 1941) and New Zealand (Hamilton, 1916 ; Phillipps, 1927).

I have examined the type of *T. pentastigma* described by Norman (1922) from Misaki, Japan, and have come to the conclusion that Matsubara (1941) was correct in synonymizing this species with *T. trachypterus*. A comparison of this specimen with one of equal length from the Mediterranean shows that there is no significant difference in vertebral or fin-ray counts. There is a difference in the proportional body depth of the two examples, the Mediterranean specimen having a slightly deeper body. This character, however, is a known variable in this group of fishes and it is also obvious from the proportions given by Norman that the Japanese example has shrunk appreciably since being examined by him. This specimen has a pattern of five dark blotches along the side of the body, whereas *T. trachypterus* has usually three to four of these markings. This is not constant, however, as several of the Mediterranean specimens which I have examined also show a pattern of five dark blotches.

It may be noted that *T. pentastigma* appears to be very similar, both in meristic counts and in markings, to *T. rex-salmonorum* described from San Francisco Bay by Jordan and Gilbert (1894) of which *T. seleniris* Snyder (1908) from Monterey Bay, California is a synonym. *T. arawatae* Clark (1880) from New Zealand may well be synonymous with the above, but these records are all outside the area covered in this paper.

There is an important error in the original description of *T. pentastigma*, Norman stating that the jaws of the specimen are without teeth. A careful examination of the holotype, however, reveals the presence of slender teeth in both jaws, the number and form of which are similar to those found in other specimens of *Trachipterus*.

The large specimen from the Mediterranean described by Günther (1861) as *T. rüppellii*, although in a poor state of preservation, is undoubtedly an adult example of *T. trachypterus*. I have been unable to find any characters that could warrant this specimen being considered specifically distinct.

Barnard (1947) mentions and figures specimens from South Africa, which he considers to be examples of *T. trachypterus*. I include these records with some hesitation as I believe that they are more properly referable to the Australian species *T. jacksonensis*. The same author (1948) lists a fully grown female under the name *T. arcticus*. It is clear from the figure that this specimen is an example of *T. trachypterus* and Barnard himself indicates some doubt as to the specific identity of this fish. King and Ikehara (1956) record an example of *T. trachypterus* from the Central Pacific.

Fourty-four specimens have been examined, ranging in length from 81 to 1,700 mm. The coloration and markings are similar to those of the previous species.

DISTRIBUTION. Mediterranean, S. Africa, Central Pacific, Japan, New Zealand.

Zu Walters and Fitch

Zu Walters and Fitch, 1960. *Calif. Fish Game*, **46** : 445

Body elongate, laterally compressed. The caudal region sharply constricted dorso-ventrally behind the vent. Twelve to 18 strong caniniform teeth in the upper jaw, 8 to 12 in the lower jaw, with smaller teeth at the symphysis. Vomer with 4 strong teeth, both palatines with 3 teeth. Nostrils as in *Trachipterus*. Dorsal fin consisting of 120 to 150 rays, the first 5 elongate. Pectorals with 11 to 12 rays, pelvics with 3 to 6 rays, present at all stages. No anal fin. Caudal fin in two parts, the upper fan-like of 8 to 12 rays, the lower of 1 to 5 rays. These latter are reduced, but are not rudimentary as in *Trachipterus*. Ventral edge of body not covered with wart-like tubercles. Lateral line armed, straight as far as the ventral constriction where it joins the lower edge of the body. Posteriorly from this point the ventral edge of the caudal region is armed with an additional paired series of downwardly directed spines, one on either side of the body. Deciduous cycloid scales present. Gill-rakers on first arch $3 + 1 + 8$. Branchiostegal rays, 6. Vertebrae, 64–65. Swim bladder present, though much reduced in adults. In young stages bulbous flaps are present on the elongate dorsal and pelvic rays.

Type : *Trachypterus cristatus* Bonelli, 1820.

DISTRIBUTION. Mediterranean ; S. Atlantic ; Indo-Pacific ; Japan.

Closely related to *Trachipterus*, from which it differs in having fewer vertebrae and a stronger dentition, in the presence of scales and in the shape of the ventral profile of the body and of the caudal fin.

Zu cristatus (Bonelli)

Trachypterus cristatus Bonelli, 1820. *Mem. Acad. Sci. Turin*, **24** : 487 (Gulf of Spezia) ; Günther, 1861. *Cat. Fish. Brit. Mus.* **3** : 301 (description) ; Giglioli, 1880. *Elenco dei Mammiferi, etc.* : 91 (Nice) ; Moreau, 1881. *Hist. nat. Poissons*, **2** : 567 (description, distribution) ; Carus, 1889–1893. *Prod. Faun. Médit.* : 700 (description, distribution) ; Goode and Bean, 1895. *Oceanic Ichth.* : 479 (description, distribution) ; Parona, 1898. *Atti Soc. Ligur. Sci. Genova*, **9** : 350 (Ligurian Sea) ; Fage, 1907. *Arch. Zool. exp. gén.* (4) **7** : 73 (listed from Balearic Islands) ; Sanzo, 1918. *Mem. R. Como Talass. ital. Venice*, **64** : 1–15 (eggs and larvae) ; Argilas, 1928. *Bull. Sta. Aquic. Pêche Castiglione Fasc.* **1** : 27, 2 figs. (Algeria) ; Sparta, 1931. *Fauna e Flora del Golfo di Napoli*, **38** : 272 (young stages) ; Stephanidis, 1939. *Acta Inst. Mus. zool. Univ. Athens*, **2** : 246, fig. (Greek waters) ; Lozano y Rey, 1947. *Mem. R. Acad. Cienc. Madrid*, **9** : 689 (description, distribution) ; Smith, 1949. *Ann. Mag. nat. Hist.* (12) **2** : 99 (Durban) ; Smith, 1949. *Sea Fishes of Southern Africa* : 142, fig. (description, distribution) ; Tortonese and Trotti, 1950. *Atti Acad. Ligure*, **6** : 99 (Gulf of Spezia) ; Dieuzeide, Novella and Roland, 1954. *Bull. Sta. Aquic. Pêche Castiglione* (N.S.), No. 5 : 151, figs. (Algeria) ; Tortonese, 1958. *Doriana*, **2**, No. 89 : 1–5 (Ligurian Sea).

Gymnetrus repandus Metaxa, 1833. *Ann. Med. Chirug. Roma Fasc.* **1** : 53 (Gulf of Naples).

Trachypterus bonelli Cuvier and Valenciennes, 1835. *Hist. nat. Poissons*, **10** : 331 (Mediterranean) ; Canestrini, 1862. *Arch. Zool. Anat. Fis. Genova*, **1**, Fasc. 1 : 266 (Gulf of Genoa).

Gymnetrus müllerianus Risso, 1840. *Arch. naturgesch. Berlin*, **6** : 13 (Nice).

Trachypterus repandus, Costa, 1850. *Fauna Regn. Napoli*, **2** : 11, pl. (Mediterranean) ; Bonaparte, 1846. *Cat. met. Pesci Europei* : 79 (synonymy) ; Steindachner, 1868. *S.K. Akad. Wiss. Wien*, **57** : 676 (Alicante) ; Canestrini, 1871–72. *Fauna d'Italia Pesci* : 194 (description) ; Giglioli, 1880. *Elenco dei Mammiferi, etc.* : 92 (Naples) ; Goode and Bean, 1895. *Oceanic Ichth.* : 480 (description) ; Pietschmann, 1925. *Veröff. naturhist. Mus. Wien*, **5** : figs. 1–3.

Trachypterus iris Buen (nec Walbaum), 1917. *Bol. Pesca Madrid*, **2** : 23–26, 2 figs. (description, distribution).

Trachypterus gavardi Bounhiol in Bounhiol and Gavard, 1923. *Bull. Inst. Oceanogr. Monaco*, No. 432 : 1–4 (Bay of Algiers) ; Weber and de Beaufort, 1929. *Fishes of the Indo-Australian Archipelago*, **5** : 91 (references).

D. 120–150 ; A. 0 ; V. 6 ; P. 11 ; C. 8 + 4 ; Branchiostegal rays 6 ; Vertebrae 64–65 ; Gill rakers 3 + 1 + 8.

This species is markedly different from both species of *Trachipterus*, as indicated in the generic description. The most obvious character is the shape of the ventral profile, which is scalloped and sharply constricted at the vent in this species, a difference which is present in specimens of 30 mm. length upwards. It would appear to attain to the same length as *T. trachypterus*, the longest specimen I have seen recorded being 1,105 mm. in total length. This specimen was captured near Genoa and reported on by Tortonese (1958). The body in this species is more robust and the dentition stronger than in *Trachipterus*.

Zu cristatus is found in the Mediterranean, from which area all stages have been taken on numerous occasions. Outside the Mediterranean it has been reported from Madeira and the Azores, with one record from Durban, S. Africa.

I have examined a larval form 32 mm. in standard length, taken by the " Challenger " near the Philippines and reported on by Günther (1887) and another specimen 31 mm. in standard length, taken by the " Discovery " off the Cape of Good Hope (33° 30′ S., 17° 29′ E.). Both these specimens are morphometrically indistinguishable from *Zu cristatus*, and it may be that the genus *Zu* is monotypic. Confirmation of this fact, however, must be left for Walters *et al.* It is for this reason that I have not included *T. ijimae* Jordan and Snyder 1901 from Japan or *T. semiphorus* Bleeker 1868 from Amboina in the synonymy of *Zu cristatus*.

The colour pattern of this species is quite distinctive and consists of six or seven incomplete dark wavy vertical bars dorsally, with three or four similar markings on the ventral edge of the body. On the caudal region there are six or seven entire vertical dark bands. The body is silvery, as in *Trachipterus*, but with the addition of deciduous cycloid scales. The caudal fin is usually dark brown to black in preserved material.

Twenty-six specimens have been examined, ranging in length from 31 to 655 mm.

DISTRIBUTION. Mediterranean, Madeira, Azores, Durban, ? Cape of Good Hope, ? Philippines, ? New Zealand.

Young stages of Trachipterid fishes

Having had the opportunity of examining a number of young examples of each of the three species dealt with here, it is evident that the characters present in the young of this group persist until a definite developmental stage is attained. This does not appear to be directly correlated with size alone, as in some instances smaller sized individuals show fewer juvenile characters than other specimens of larger size. In the majority of specimens examined, this change takes place within the size limits of 50 and 70 mm. On the other hand, there is an example of the genus *Zu* from the Philippines of 38 mm. length in which almost all trace of the juvenile characters has already been lost. This suggests that the post larvae are pelagic and that a triggering process is needed to set in motion this partial metamorphosis.

In specimens prior to this stage, the first 5 or 6 dorsal rays and the first 3 or 4 pelvic rays are greatly elongated, the caudal fin is still parallel to the body axis and has not yet separated into the distinct upper and lower lobes found in the adult. Not all the pectoral rays are fully ossified and this applies also to the rays of the dorsal fin. Posteriorly there is a fin fold supported by actinotrichia. On the ventral surface, opposite this posterior part of the dorsal fin, is a similar lobe. As members of the family Trachipteridae do not possess an anal fin, the very numerous and closely aggregated structures present in this ventral lobe, which show no basal supports, are probably actinotrichia giving added strength to this structure whilst it is of use to the larvae. Later, during the transitional stage from larva to adult, the lobe is probably sloughed off or resorbed.

This is the condition mentioned by Clarke (1880) in his description of *T. arawatae* from New Zealand. These two lobes, which he describes as dorsal and anal adipose fins, are the main characters used to distinguish this form from related species. It should be noted that these larval characters were still present in Clarke's specimen, which had attained a length of 65 mm. Ehrenbaum (1905) mentions the presence of these lobes and both Emery (1879) and Smitt (1893) indicate the presence of a similar structure in their figures of the young stages of *T. trachypterus*.

Finally, there is the growth that occurs in the vertebral column. In the juvenile stages the caudal vertebrae are the same length as those anteriorly, but with growth they elongate until in the adult they become two to four times as long as the anterior vertebrae.

Sexual dimorphism in the Trachipteridae

Although sexual dimorphism may be present in this group of fishes, I have not been able to show its occurrence from the material available to me. Attention must be drawn, however, to the statement made by McCann (1953) in which he says that such dimorphism does occur, as he has based these remarks on quite erroneous grounds. He figures two undoubted examples of the genus *Zu* and comments on other previously described specimens of the same genus, all of which he regards as males of *Trachipterus arcticus*, on the basis of a dissection made on one example of what he terms an aberrant juvenile form.

Food of Trachipterid Fishes

A few authors have commented on the food of these fishes, although the majority of those captured usually have an empty gut. It is clear, however, that they are carnivorous. Moreau (1881) states that they feed on molluscs and small crustaceans. McCann (*l.c.*) states that he has found the "whitebait" stage of other fishes in stomach contents of *Trachipterus* taken in New Zealand waters. Of the fifty or so specimens which I have had the opportunity of examining, only three contained identifiable remains in the gut. These consisted of a fairly complete example of an isospondylid fish, *Microstoma* sp., from a specimen taken off Madeira ; a mass of penaeid prawns, *Penaeus duodecimalis*, and several squid beaks, probably *Loligo*, from two further specimens taken in the Mediterranean.

Swim Bladder

It is known that the fishes of the order Allotriognathi possess a physoclistic swim bladder (Regan, 1907 and Berg, 1947) and this condition has been verified in the genera *Lophotes* and *Velifer*. The position appears to be somewhat uncertain, however, so far as the Trachipteridae are concerned. Of the several authors who have published accounts of the anatomy of these fishes Meek (1890), in describing an example of *T. arcticus*, makes no mention of the presence of a swim bladder. Other authors, notably Reid (1849), Smitt (1893) and Andryashev (1954), state quite definitely that this organ is absent. As already mentioned Regan and Berg, in their definition of the order, state that a swim bladder is present but make no further reference to it in the diagnosis of the family.

In view of these conflicting statements I have examined two or three half-grown and adult specimens of *T. arcticus*, *T. trachypterus* and *Zu cristatus* of varying sizes, together with a large example of *Regalecus* and have found that a swim bladder has been present in each specimen. It is a small rudimentary structure, having the appearance of a sac-like swelling, which lies dorsal to the oesophagus and a little

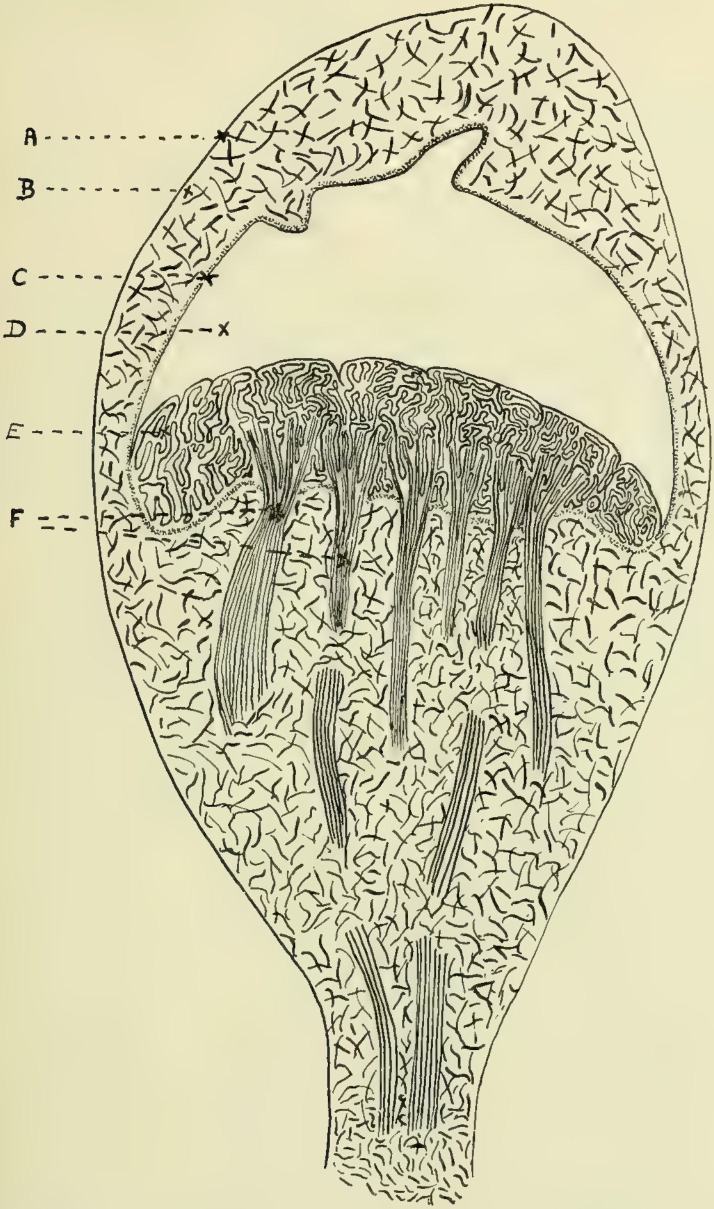

FIG. 3. Composite T.S. of swim bladder. A. tunica externa; B. submucosa; C. inner epithelium; D. lumen; E. gas gland; F. retia mirabilia.

to the right of the median line. In a specimen of *T. trachypterus* of 1,075 mm. length, the swim bladder is approximately 8 mm. long. It is, therefore, not readily visible except when dissecting the fish from the right-hand side. Stained transverse sections of this structure show quite clearly, despite the regressed condition, the presence of a gas gland with six or seven retia entering it. A small lumen is also present (Text-fig. 3).

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PLATE 62

Fig. 1. *Trachipterus arcticus.* Photograph of the holotype of *Trachipterus gryphurus* Lowe. × $\frac{1}{3}$.

Fig. 2. *Trachipterus trachypterus.* Photograph of the holotype of *Trachipterus pentastigma* Norman. × $1\frac{1}{3}$.

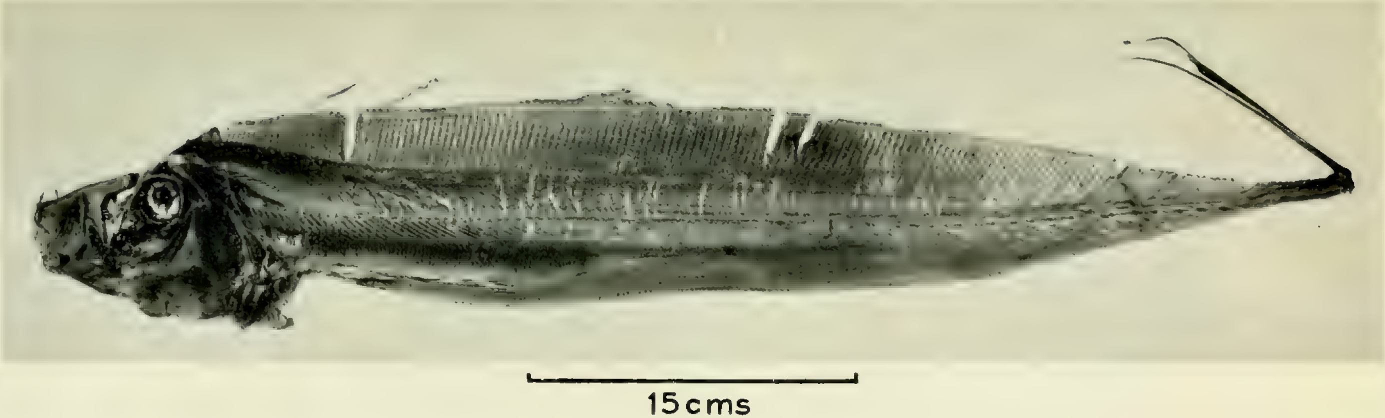

FIG. 1.

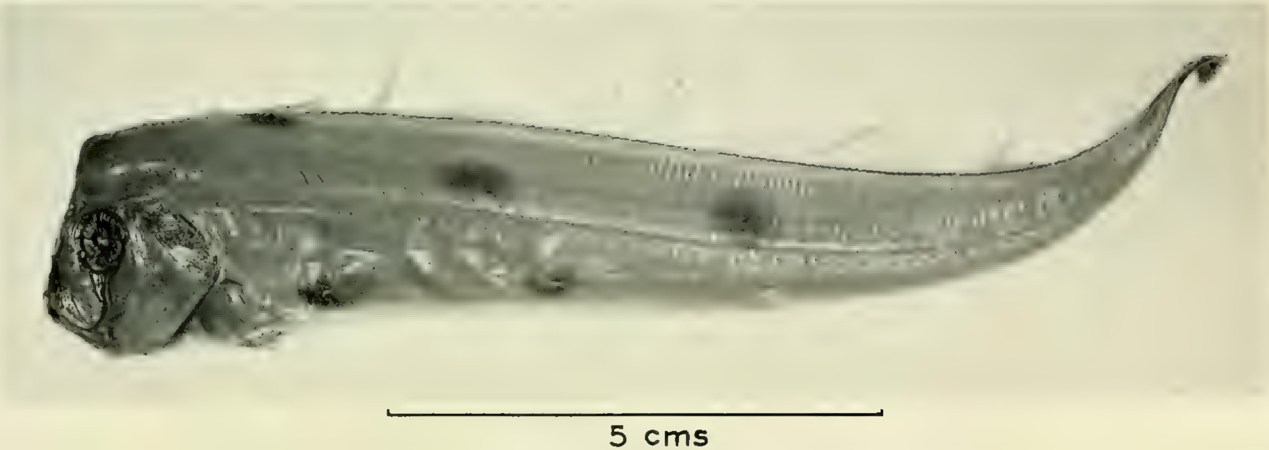

FIG. 2.

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A YOUNG *MACRISTIUM* AND THE CTENOTHRISSID FISHES

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- 3 JUL 1961

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A YOUNG *MACRISTIUM* AND THE CTENOTHRISSID FISHES

By N. B. MARSHALL

SYNOPSIS

A young fish, taken by "Discovery Investigations" in the Bay of Biscay, has proved to be the second known representative of *Macristium chavesi* Regan (1903), a species belonging to the order Isospondyli (family Macristiidae). In fin pattern, which is unique among isospondylous fishes gill cover structure, and branchiostegal ray complement, this species is very close to the ctenothrissid fishes of Cretaceous strata.

Consideration of the functional design of the fins of " lower " teoleosts with thoracic (or near thoracic) pelvic members suggests that the similarities between *Macristium* and the ctenothrissids are not likely to be due to convergent evolution. *Macristium* would thus appear to be a modern ctenothrissoid fish, a supposition to be fully tested when an adult specimen becomes available.

INTRODUCTION

In 1903, Mr. C. Tate Regan wrote a short report on some fishes brought back from the Azores by Mr. W. R. Ogilvie Grant. One fish had a quite unusual appearance, but Regan (1903) believed it to be most nearly related to Günther's genus *Bathysaurus*, " . . . which it resembles in the position of the fins and the number of rays, but with the mouth only moderately wide, the dentition weaker, the maxillary dilated posteriorly, the fin rays much prolonged, and the ventrals still more anterior in position." Regan described the fish as a new genus and species, *Macristium chavesi*, and placed it in the family Scopelidae.

When he came to revise the order Iniomi, Regan decided that closer scrutiny of the fish (which was housed in the Punta Delgada Museum in the Azores), was desirable. Having obtained the fish from Major F. A. Chaves, Regan (1911) revised his judgement of its systematic position. These were his conclusions : " Originally I believed that *Macristium* was related to *Bathysaurus* Günth, which it resembles in the position of the fins and the number of rays. I am now of the opinion that this resemblance is misleading, for I think that in all probability the praemaxillaries would not exclude the maxillaries from the gape. In any case, *Macristium* must be made the type of a distinct family, Macristiidae, probably related to the Alepocephalidae."[1]

It is clear, then, that Regan believed *Macristium* to be an isospondylous fish. In his classification of fishes, Berg (1947) puts this genus in the order Clupeiformes (=Isospondyli), suborder Clupeoidei and places it immediately after the superfamily Alepocephaloidae. But he remarks that the systematic position of the Macristiidae is uncertain. This is also Gosline's (1960) view.

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[1] Regan continues ; " Before returning the fish to the Ponta Delgada Museum it seems best to make a figure of it and to reinforce my original description." But recent correspondence has revealed that the type of *Macristium chavesi* is missing from this Museum.

When working on the Miripinnati (Bertelsen & Marshall, 1956), we were naturally interested in the " lower ", soft-rayed teleosts that have large pelvic fins set close to the pectorals. We considered *Macristium* and two Upper Cretaceous families, the Ctenothrissidae and the Chirothricidae, but concluded that the similarities in fin pattern, which are certainly not very striking, could be convergent. (We might also have included *Pantodon*, and would, no doubt, have come to the same conclusion.)

But this survey not only revealed that the Miripinnati are a natural and somewhat isolated group within an " iniomous complex ". It lead me to realize that there are striking similarities between the fin patterns of *Macristium* and the ctenothrissid fishes, which I discussed when reading a paper (unpublished) on the Miripinnati (" Some new oceanic fishes ") to the Challenger Society on 26th October, 1955.

Closer consideration can now be given to these possible, even probable indications of a relationship between *Macristium* and the Ctenothrissidae. Recently when looking through the unnamed *Discovery* Collections, I found a young *Macristium* (taken in the middle part of the Bay of Biscay (Station 2072, 46° 31·6′ N., 07° 42·9′ W., TYFH, 170 (—0) m., 22.v.1937). Making due allowance for its immaturity, the form and meristic features of this young fish are close to those of the type specimen (Regan, 1903 : 345 ; 1911 : 204–205). Treatment of these aspects must obviously form the first part of this paper. Then follows an assessment of the affinity between *Macristium* and the ctenothrissids, an enquiry which has involved some consideration of the functional significance of fin pattern in the lower soft-rayed teleosts with thoracic (or near thoracic) pelvic fins.

A young *Macristium chavesi* Regan

(Text-figs. 1–3)

Locality : *Discovery* Station 2072 ; 22.v.1937 ; 46° 31·6′ N., 07° 42·9′ W. (middle part of Bay of Biscay) ; TYFH 170 (—0) m.

Standard length of fish, 33·0 mm.; total length, 41·5 mm.

MERISTIC FEATURES

Dorsal rays, 17, the first ray a small splint closely applied to the next ray.
Anal rays, 13, the first ray splint-like.
Pectoral rays (left), 15, the uppermost ray a small splint.
Pelvic rays, 7.
Principal caudal rays, 10 + 9.
(None of the fin-rays is branched.)
Branchiostegal rays, 10.
Gill rakers on first arch, 3 + 1 + 13.
Number of myotomes, 61.

MEASUREMENTS (mm.) and proportions (in parentheses and expressed as percentages of the standard length).

1. *Head*. Length, 6·5 mm. (19·7) ; length of snout, 2·1 (6·4) ; interorbital width, *c.* 2·0 (6·0) ; horizontal diameter of eye, 1·4 (4·2) ; length of premaxillae, 1·3 (3·9) ; length of maxillae, 2·0 (6·1) ; length of mandible, 3·3 (10·0).

2. *Body* (trunk and tail). Depth of body at origin of pelvic fins, 4·0 (12·1) ; depth at origin of anal fin, 2·8 (8·5) ; depth of caudal peduncle, 1·5 (4·5) ; length of caudal peduncle, 5·5 (16·7).

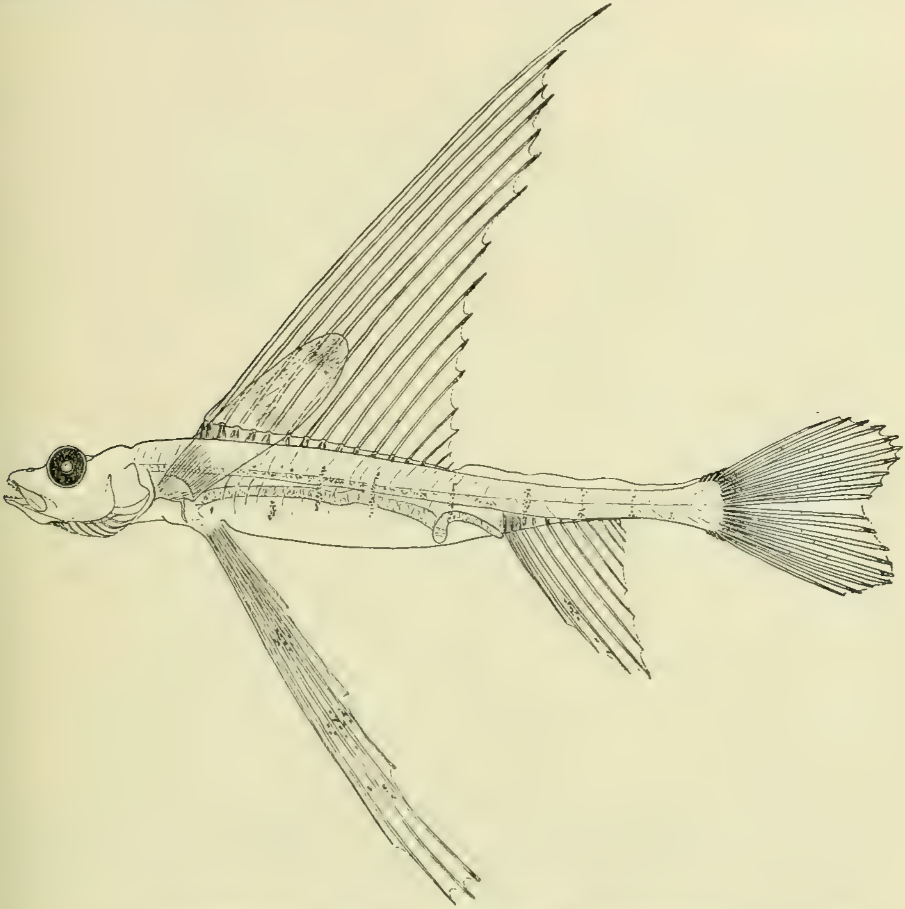

FIG. 1. *Macristium chavesi* Regan. Young fish from *Discovery* Station 2072 (×3⅕).

3. *Fin positions.* Length between tip of snout and origin of dorsal fin, 10·0 (30·3) ; snout to origin of anal fin, 23·5 (71·2) ; snout to origin of pectoral fins, 7·5 (22·7) ; snout to origin of pelvic fins, 9·0 (27·2).

4. *Fin size.* Length of base of dorsal fin, 12·0 (37·9) ; length of longest dorsal ray (2nd), 27·0 (81·8) ; length of base of anal fin, 5·0 (15·2) ; length of longest anal ray (5th), 9·0 (27·3) ; length of longest pectoral rays (middle), 10·0 (30·3) ; length of longest caudal rays, 8·5 (25·8) ; length of longest pelvic rays (2nd to 4th), 21·0 (63·7).

FIN PATTERN

The most striking features are the high, sail-like dorsal fin and the very extended pelvic fins, which have a thoracic setting (in this young fish there appears to be no attachment of pelvic to pectoral girdle). There is a regular and fairly sharp decrease in the height of the dorsal fin after the longest (2nd) ray, the length of which is about four-fifths of the standard length. The base of the fin extends along the greater part of the trunk region (along rather less than half the combined extent of trunk and tail). The longest rays of the pelvic fins (2nd to 4th) are just over three-quarters the length of the second dorsal ray, and when applied along the body, extend to about the middle of the caudal peduncle. The dorsal and pelvic fins arise at precisely opposite points. A line joining their origins would come just behind the muscular bases of the pectoral fins, the rays of which are closely associated, forming relatively long, paddle-shaped fins. The triangular anal fin originates 7 myotomes behind the last dorsal ray, but this separation may be reduced when the dorsal fin is fully formed (see p. 361). The longest rays of the anal and caudal fins are about equal in length and are slightly shorter than the longest pectoral rays.

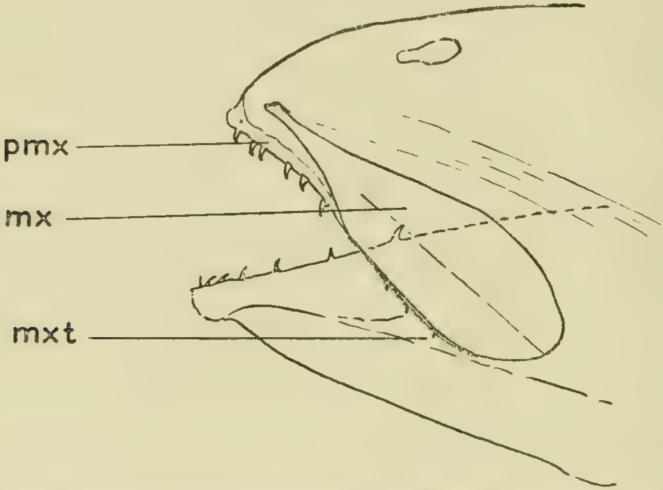

FIG. 2. Jaws of *Discovery Macristium chavesi* (×28). *pmx*, premaxilla; *mx*, maxilla; *mxt*, maxillary tooth.

SCALES

The skin is without any trace of scaling.

JAWS AND DENTITION

The premaxillae and maxillae together form the biting edge of the upper jaw, their contributions being about equal in extent (see Text-fig. 2). The maxillae are paddle-shaped, the greatest width of the blade being about one-third the length of the bone.

They end just before the most forward parts of the eyes. The hinge between the lower jaw and the suspensorium lies vertically under the middle region of the eyes. The width of the jaw at the coronoid process is about one-third the length of the mandible. Upper and lower jaw bones meet in a gape that is directed upwards and makes an angle of about 40° with the long axis of the body.

Teeth are formed on the premaxillae, maxillae, dentaries, vomer, palatines and tongue. They are pointed and recurved and are fairly large compared to the bones that bear them. Each premaxilla has about 6 teeth. There is about the samen umber of larger recurved teeth forming an inner row on each dentary. The outer row consists of about 10 teeth, which are about half the size of the inner members, A few teeth can just be seen emerging from the dental lamina of each maxilla. The vomer bears 6 teeth (3 on each side), these being slightly larger than the premaxillary teeth. Each palatine carries 3 teeth. The spatulate tongue is armed with a transverse row of 3 pointed, retrorse teeth, which emerge fairly close to the anterior border of this organ.

PSEUDOBRANCHIAE

Present.

BRAIN AND SENSE ORGANS

The mid-brain is large compared to the forebrain, which contains the olfactory bulbs. The cerebellum is moderately well developed (Text-fig. 3).

The opening into each nasal sac is a single keyhole-shaped aperture. (As Regan, 1911 definitely states that there are 2 nostrils on either side of the snout, these must be formed at a later stage.)

INTERNAL ORGANS

The intestine is quite straight except for a turn just before the anus (see Text-fig. 1). There is no evidence of a swimbladder.

MUSCULATURE

Except for the uppermost parts of the hypaxial myotomes (which arch over the body cavity) this lower part of the body musculature is quite undeveloped. The lateral and ventral walls of the body cavity are thus perfectly transparent (for the pigmentation is also in a larval condition).

PIGMENTATION

The most conspicuous features are 7 narrow, vertical bars of pigment, 3 being on the trunk and 4 on the tail. The first bar, which does not extend above the horizontal septum, is vertically under the 7th dorsal ray ; the second under the 9th, the third under 12th, and the fourth under the last dorsal ray. The fifth pigment bar is opposite the 2nd anal ray, the sixth between the 8th and 9th anal rays, and the seventh is not far behind the last anal ray. There is also a narrow horizontal tract of melanophores running just below the horizontal septum. (It begins just behind the head and ends just before the anus.) There are 3 patches of pigment on the pelvic fins (see Text-fig. 1) and scattered cells on the webs between the 3rd and 4th anal rays. There is a fine peppering of small melanophores over the bases of the caudal rays.

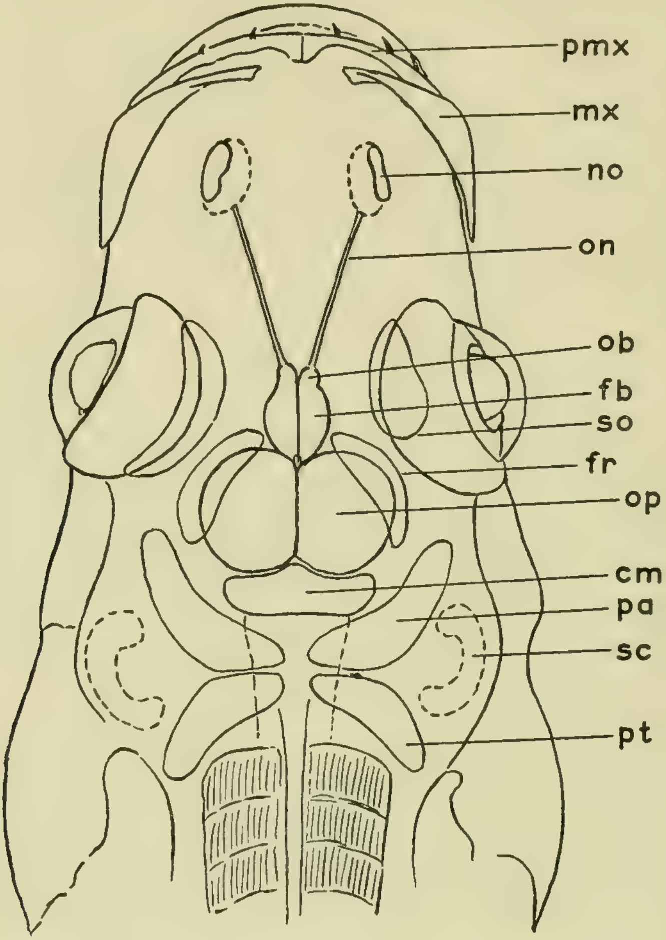

FIG. 3. Dorsal view of head of Discovery *Macristium chavesi* (×21). *pmx*, premaxilla; *mx*, maxilla; *no*, nostril; *on*, olfactory nerve; *ob*, olfactory bulb; *fb*, forebrain; *so*, supraoccipital bone; *fr*, frontal bone; *op*, optic tectum; *cm*, cerebellum; *pa*, parietal bone; *sc*, semicircular canal; *pt*, post-temporal bone.

Comparison of this description with those given by Regan (1903 and 1911) indicates that this young fish belongs to the genus *Macristium* and, most likely, to the species *chavesi*, Relevant comparative data will be found in Table I.

TABLE I.—*Comparison of Type of* Macristium chavesi *Regan with* Discovery *Specimen*

	Type specimen (Regan, 1903 and 1911)	*Discovery* specimen
Standard length (S.L.)	110 mm.	33 mm.
Fin-ray formula	D. 18; A. 12; Pct. 16; Pv. 8. Principal caudal rays 10+9	D. 17; A. 13; Pct. 14; Pv. 7. Principal caudal rays 10+9
Number of myotomes	About 62	61
Number of branchiostegal rays	About 8	10
Proportions:		
Depth body into S.L.	$7\frac{1}{2}$	$8\frac{1}{4}$
Length head into S.L.	5	5
Eye diameter into head	Nearly 8	$4\frac{2}{3}$
Interorbital width into head	$3\frac{1}{3}$	*c.* 3
Base of dorsal fin into S.L.	$2\frac{1}{4}$	$2\frac{3}{4}$
Posterior extent of maxillae	To anterior quarter of eye	To anterior rim of orbit
Origin of anal fin	Just behind last dorsal ray	Well behind (6 myotomes) last dorsal ray

Scrutiny of this Table will reveal that the fin-ray and myotome numbers of the type are quite close to those of the *Discovery* specimen. The one outstanding difference in the proportional data concerns the eye diameter, which is slightly less than one-eighth of the head length in the type and almost equal to one-quarter of this dimension in the *Discovery* fish. However, the type (standard length, 110 mm.) is more than three times as large as the present specimen (S.L., 33 mm.), and it is a general rule that the relative size of the eyes decreases with growth, particularly during the earlier life-history of fishes. Even so, the difference is more than that usually found within any given species.

Reference to Text-fig. 4 will also show that the eyes of the type specimen are set well below the interorbital level (not projecting above, as in the *Discovery* specimen). Yet Regan (1911) states that the frontals are slightly raised above the eyes, which may well be a structural indication of the earlier position and proportionately greater size of these sense organs. If we also consider the damaged, and presumably shrunken, condition of the type specimen, which Regan (1911) thought might have been washed ashore, the divergence between the relative eye sizes seems more comprehensible.

The type specimen of *Macristium chavesi* is also somewhat deeper bodied than the *Discovery* fish and has a relatively longer base to the dorsal fin. This last difference may be coupled with another: according to Regan's (1911) figure the last dorsal ray appears to be no more than one myotome in advance of the first anal ray, whereas in the *Discovery* specimen the separation between these 2 rays is about 6 myotomes. However, Regan (1903) remarks that the anal fin begins " . . . directly behind the vent, which is slightly posterior to the last dorsal ray." The separation between the last dorsal and the first anal ray may thus be somewhat greater than that shown in his (1911) figure. Furthermore, the last few dorsal rays of the *Discovery* fish are in a very early stage of development, and it may well be that at a later stage the gap between the 2 fins will close. Considerable changes in fin pattern, involving both position and extension of a fin base are not uncommon during the early life-history

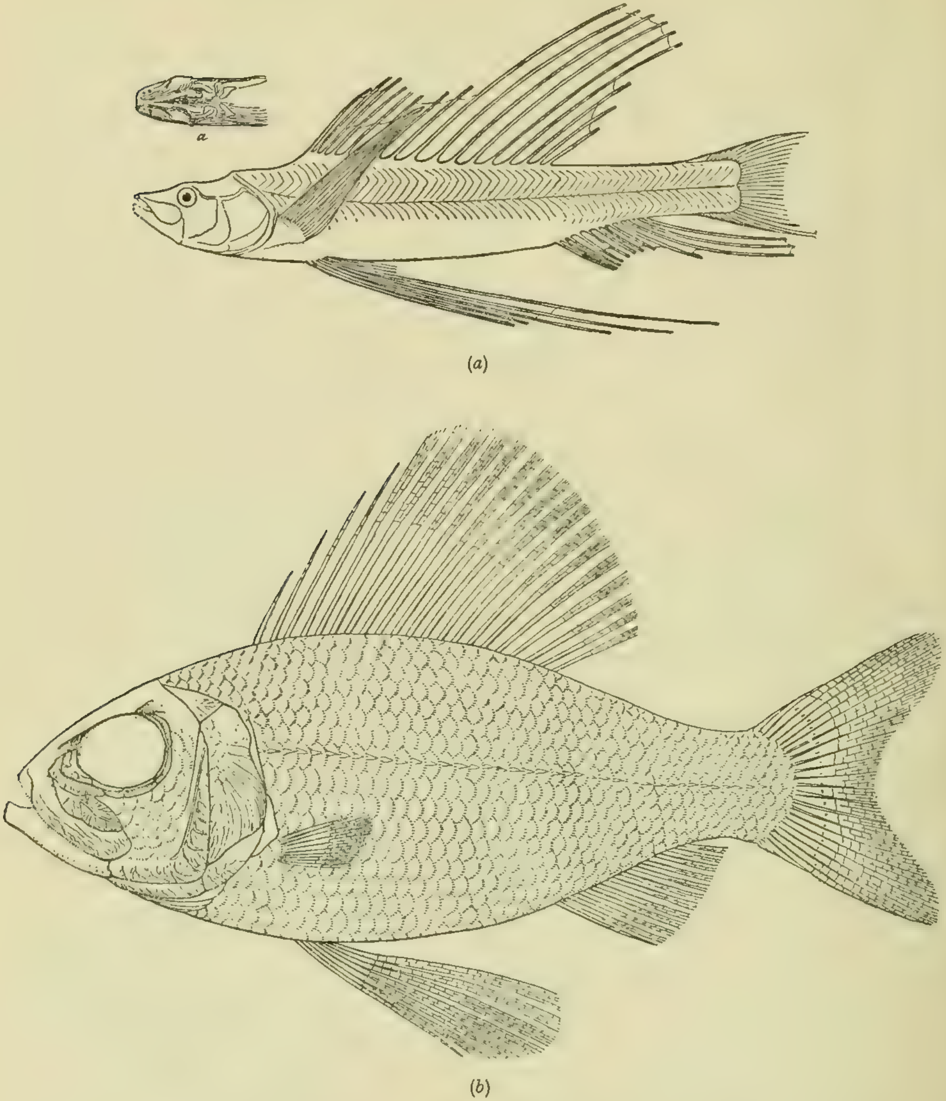

FIG. 4. (*a*) *Macristium chavesi* Type specimen (from Regan, 1911). Reproduced by kind permission of Taylor & Francis, Ltd. (*b*) *Ctenothrissa radians* (Agassiz) (from Woodward, 1903). Reproduced by kind permission of the Council of the Palaeontographical Society.

of teleosts. (In the sprat (*Sprattus sprattus*), for instance, the gap between the last dorsal ray and the first anal ray decreases by 3 or 4 myotomes between post-larval and adolescent stages.)

Apart from this dorsal-anal gap, there is very close agreement between the fin position of both fishes (see Text-fig. 4). There are, however, differences in fin form. In the type the posterior parts of the dorsal and anal fins are far better developed than those of the *Discovery* fish. Yet, as already stated, the last few dorsal fin rays, and also the last few anal rays, are in a very early stage of formation. The 5th pelvic ray of the type, which appears to be complete, extends beyond the caudal peduncle, being thus much " in advance " of the corresponding ray of the other fish. But again the difference may be no more than that associated with particular phases of development.

To conclude, having an awareness that the *Discovery* fish is little more than post-larval in phase, there is no good reason for considering it to represent a second species of *Macristium*. When the life-history of *M. chavesi* is adequately known we may expect this young fish to fall into place in the earlier and more active phases, times during which there are trenchant changes in form and function.

MACRISTIUM AND THE CTENOTHRISSID FISHES

Despite the thoracic position of their pelvic fins, Woodward (1903), considered the Ctenothrissidae to be closely related to the existing Clupeidae. In his (1901) *Catalogue of the Fossil Fishes in the British Museum* (*Natural History*), the synopsis of Cretaceous and Tertiary Isospondyli (p. 5) shows that besides the difference in position of the pelvic fins, the two families can be distinguished in that the abdominal vertebrae of the ctenothrissids lack transverse processes. Reference to the definitions of the families (Ctenothrissidae, p. 119 ; Clupeidae, p. 128) also reveals that there is some median contact between the parietal bones of the first-named fishes. In the clupeids these two skull bones are completely separated by a well-formed supraoccipital. The outstanding common features of the two families (taken from these definitions) are as follows : " Premaxilla small and maxilla relatively large and loose, both these bones entering the upper border of the mouth ; two supramaxillaries ; teeth acuminate, but feeble. Opercular apparatus complete, but few branchiostegal rays and no gular plate. Vertebral centra well ossified ; ribs nearly or completely encircling the abdominal cavity. Fin fulcra absent. Post-temporal bones in contact with postero-lateral angles of cranium ; post-clavicular plate (post-cleithrum) overlapping the clavicle (cleithrum)."

Berg (1947) must have been more impressed by the difference in fin pattern, for in proposing a new suborder Ctenothrissoidei (p. 422) he states that these fishes are " As Clupeidae but with very large ventral fins situated *below the pectorals* " (his italics). This would seem a reasonable proposal, but whatever the opinion, we can at least agree that the ctenothrissids are isospondylous fishes, having soft-rayed fins, a caudal fin with 19 principal rays and an upper jaw bordered by both premaxillae and maxillae. By the same combination of characters. *Macristium* can also be placed in the Isospondyli. Indeed, as already quoted (p. 355) Regan (1911) considered this genus to be most closely related to the Alepocephalidae, a family that can be reasonably assigned to the suborder Clupeoidea.

Concerning closer comparisons, the most striking resemblance between *Macristium* and the Ctenothrissidae is in fin pattern (see Text-fig. 4). The tall sail-like dorsal fin, extending over the greater part of the trunk ; the long, wing-shaped pelvic fins, which arise at points opposite, or nearly opposite to the origin of the dorsal fin ; the smaller pectoral fins, set laterally on the shoulders between the lateral line and the base of the pelvics ; the rather prominent anal fin, beginning close behind the last dorsal ray and spanning about half the length of the tail ; the well-formed shallow-forked caudal fin—these are the outstanding similarities.

This precise form of fin pattern is unique within the order Isospondyli (the nearest, but not very close, approach is with *Pantodon*). Indeed it is almost without parallel among the entire complex of " lower ", soft-rayed teleosts (Isospondyli, Ostariophysi, Haplomi, Iniomi, Cetunculi, Miripinnati, Chondobrachii, Giganturoidea and Lyomeri). One striking convergence of fin pattern is with *Bathysaurus* , a congruence that first led Regan (1903) to suspect a relationship between *Macristium* and this genus (now assigned to the order Iniomi, suborder Myctophoidea, family Bathysauridae). In fact, the *Macristium*-ctenothrissid fin pattern most nearly resembles that of one particular species, *Bathysaurus ferox.* But the term fin pattern, as used by Harris (1953), includes both fin position and fin form. Now the fin positions of *B. ferox* are like those of *Macristium* and *Ctenothrissa* (except that the origin of the dorsal fin is behind the pelvic insertions in the former). In fin form, however, *B. ferox* has less accentuated dorsal and pelvic fins.

There is also a close resemblance between the fin pattern of another iniomous species, *Latropiscus purpurissatus* (Aulopidae) and that of *Macristium* and *Ctenothrissa.* In this aulopid the pelvic fins do arise at points opposite to the origin of the dorsal fin, but again, both kinds of fins are less expansive than those of the two genera in question. The aulopids also have an adipose dorsal fin, which is certainly absent in *Macristium.*

Macristium and *Ctenothrissa* are not only alike in fin pattern, but also in fin-ray numbers, which are listed below in Table II. The figures for *Ctenothrissa* are taken from Woodward (1901 and 1903).

TABLE II.—*Fin-ray Numbers of* Macristium chavesi *and* Ctenothrissa *spp.*

Species	Dorsal	Anal	Pectoral	Pelvic
Macristium chavesi .	17–18	12–13	16–18	7–8
Ctenothrissa radians .	20–25	12+	10–12	7–8
C. vexillifer . . .	18–20	13–14	?	8
C. microcephala . .	?	*c.* 10	*c.* 10	8–9

It will be evident that there is a close correspondence between the numbers of anal and pelvic rays and a fairly near match in dorsal ray complements. There is a bigger gap in the numbers of pectoral rays, but in *Ctenothrissa* the pectorals are rather weakly developed. *Aulolepis*, the other known genus of ctenothrissid fishes, also had small and delicate pectoral fins, each with about 12 rays, while there are 9 rays in the pelvics (Woodward, 1903).

Apart from upper jaws bordered by both the premaxillae and maxillae, there are numerous other similarities between the head structure of *Macristium* and the Ctenothrissidae. The underlying structural congruence is in the markedly forward inclination of the suspensoria. The jaws are thus relatively short, the hinges of the mandible and the ends of the maxillae lying below the orbits. The mandible is not only short but deep, the width at the coronoid process being about a third of the mandibular length in *Macristium* and nearly one-half this dimension in *Ctenothrissa*.

Conforming to the inclination of the suspensoria, the preopercular bones are ⅃-shaped. The divisions between the large opercular and much smaller subopercular bones run backwards and upwards from the angles of the preopercula. The interopercular bones lie below the horizontal preopercular limbs (see Text-fig. 1). There is, in fact, a close correspondence between the gill-cover bone patterns of all three genera, *Macristium*, *Ctenothrissa* and *Aulolepis*. (see also Text-fig. 4).

Macristium and *Ctenothrissa* also have much the same number of branchiostegal rays. Regan (1911) stated that there are about 8 on either side of the type of *Macristium chavesi* : the *Discovery* specimen has 10. In his descriptions of *Ctenothrissa radians*, Woodward (1903 : 81) remarks that " the number of branchiostegal rays is uncertain, but there cannot have been less than eight, perhaps ten."

Turning now to differences, the most obvious one is the lack of scales in *Macristium*. In the ctenothrissids the scales are large and regularly arranged, their edges being pectinated in *Ctenothrissa* but smooth in *Aulolepis*. A second striking difference is the development of 2 well-formed supramaxillae in the Ctenothrissidae, whereas in *Macristium* the paddle-shaped maxilla is apparently a single bone. Furthermore, the large blade-like maxillae of the ctenothrissids form two-thirds to three-quarters of the biting edge of the upper jaw, but in the *Discovery Macristium* the fraction is no more than one half. Thirdly, except for the first 4 dorsal rays, the upper pectoral ray, the outer pelvic ray, the 1st anal ray and the outer principal caudal rays, the fin rays of *Ctenothrissa* are branched. In the *Discovery Macristium* none of the fin-rays is branched, and the same appears to be true of the type specimen (Regan, 1911). Lastly there is one appreciable meristic difference. In *Ctenothrissa* and *Aulolepis* the vertebral numbers are from about 30 to 40 ; in *Macristium* there are about 60.

The significance of these contrasting features can only be properly assessed with an awareness that the *Discovery* and type specimens are young fishes. In both the skull is at an early stage of development (see Text-figs. 3 and 4) and in the former specimen, at least, this is also true of the hypaxial musculature of the trunk region. Regarding the type specimen, Regan (1911) noticed that the abdomen appeared to be very distensible, which either suggests incomplete development of the investing musculature or a poor state of preservation.

Finally, the melanophore pattern of the *Discovery* fish seems to be in a post-larval condition, there being no general pigmentation of the skin, such as appears at metamorphosis.

Considering now the first difference, the complete lack of scales in young *Macristium* need not imply their absence in the adult. In the Scopelarchidae and certain Paralepididae, for instance, the scales do not begin to form until a relatively late stage in the life-history. At first sight, indeed, young *Macristium* remind one of the *Benthalbella* larvae of scopelarchids. But it is not the absence of scales in relatively large young that provokes the reminiscence, but rather the translucent, muscle-lacking walls of the abdominal cavity. It is reasonable to assume that in fishes with this large type of post-larva the early part of the life-history is prolonged, the rate of differentiation of the organ systems being slow compared to the growth in size. In fact, young *Macristium* may not reach the adolescent stage until they are about 6 inches in length. This could well account for the non-branched condition of the fin rays of the two specimens of *Macristium* (in *Benthalbella* larvae almost all of the fin rays are in this stage of development).

The relatively small (half) share of the maxillae in the biting edge of the upper jaw could also be a larval feature. In just metamorphosed larvae of *Elops*, for instance, this maxillary fraction is between a half and two-thirds, whereas in the adult it is somewhat greater than two-thirds. Could the absence of supramaxillae simply be due to the fact that they have not yet ossified? There is no trace of supramaxillae in the above larvae of *Elops*. If, as seems likely, the early (pre-adolescent) development of *Macristium* is much protracted, the relatively late appearance of certain adult jaw features is by no means impossible. But we can only await the capture of further stages in what is clearly a most interesting kind of life-history.

Lastly, the marked difference in vertebral numbers (about 60 in *Macristium*, 30–40 in the Ctenothrissidae) need not imply marked genetic separation. Instances of a wide range of vertebral numbers *within one family* are not uncommon and, as in the fishes under review, this may be coupled with relatively small variations in the numbers of fin rays. In the Chlorophthalmidae of the Western North Atlantic the fin formula is D. 10–11, A. 7–9, Pct. 15–17, Pv. 8–9, but the vertebrae vary from 38 to 49 (Mead, in the press). There are 45–66 vertebrae in the Scopelosauridae but the usual numbers of rays are : D. 10–12, A. 17–20, Pct. 10–12, Pv. 8–10 (Marshall, in the press).

FIN PATTERNS OF "LOWER" SOFT-RAYED TELEOSTS WITH THORACIC (OR NEAR THORACIC) PELVIC FINS : FUNCTIONAL ASPECTS AND CONVERGENCE

Macristium and the Ctenothrissidae are thus closely similar in head structure and fin pattern, the latter being unique within the order Isospondyli. But could these common features be simply due to convergence? More precisely, have these features been independently acquired? And could they be adaptations to a particular way of life? If such questions could be answered in the negative, one could feel more certain of the genetic affinity between the two.

We have already seen that the *Macristium* type of fin pattern is found in two iniomous fishes, *Bathysaurus ferox* and *Latropiscus purpurissatus*. There is also a remarkable resemblance in the numbers of fin rays, which are as follows :

Macristium chavesi	D. 17–18, A. 12–13, Pct. 15–16, Pv. 7–8
Bathysaurus ferox (Type) . . .	D. 18, A. 12, Pct. 14, Pv. 8
Latropiscus purpurissatus (one specimen) .	D. 20, A. 12, Pct. 14, Pv. 9

Concerning the two iniomous species, the differences between them, particularly in head structure, are no less striking than the foregoing resemblances. The Bathysauridae and Aulopidae have clearly diverged considerably from their point of common origin, which must be close to the origin (or origins) of the iniomous fishes. Now the fin pattern of most Iniomi suggests that the ancestral fish(es) would have had a short based dorsal fin and abdominal pelvics. If this is so, then the fin array of the two above species could well have been acquired independently (and not be an instance of parallelism). Could the same be true of *Macristium* and *Ctenothrissa*? Before trying to answer this question, some consideration of certain functional aspects of fin pattern in isospondylous and iniomous fishes with thoracic (or near thoracic) pelvic fins will be relevant.

All the members of one suborder of Iniomi, the Alepisauroidea, have abdominal pelvic fins. In the other suborder, the Myctophoidea, only the Myctophidae, the Harpadontidae and the Scopelosauridae can be said to have typically abdominal pelvic fins. In the remaining families, the Aulopidae, the Chlorophthalmidae, the Bathypteroidea, the Ipnopidae, the Bathysauridae and the Synodontidae, these fins are either thoracic in position or inserted well forward on the abdomen, close to the bases of the pectorals. There would thus appear to be a correlation between pelvic fin position and habit. The bathypelagic Iniomi have abdominal pelvics whereas in all but one of the benthic groups (the Harpadontidae), the pelvics have moved near or very near to the pectorals, which have a lateral setting.

In the percoid fishes Harris (1953) has shown that lateral pectoral fins, acting in concert with thoracic pelvics, form an extremely efficient and stable braking system. He also writes : " It is interesting to find that the percoid facies has been evolved at least three times over, since it appears in the Permian Palaeoniscoid, *Dorypterus*, possibly in some Holostei (*Dapedius*) and also in the isospondyl *Ctenothrissa* ; all are short, thin, deep-bodied forms where pitching motions would be liable to become excessive during braking if it were not for this pelvic fin migration."

But this disposition of the paired fins is not necessaily an invariable indication of a braking system. Keeping to the Iniomi, the lizard-fishes (Synodontidae) have the habit of lying on the sea floor, propped up by their pelvic fins, which are inserted well forward, between the origins of the pectoral and dorsal fins. A *Trachinocephalus* in just this posture is figured by Ray & Ciampi (1958 : 190, fig. 96). As these authors remark (p. 189) : " All the lizard fishes are fiercely predatory. They sit on the bottom, resting on their ventral (pelvic) fins until some unsuspecting fish or crustacean swims by. Then they rush so quickly at the prey that the movement can hardly be seen. They prefer sand bottoms but many may be found about reefs and rocks as well as over mud and grass.

" This is one of the groups in which the normal swimming pattern has been altered. For sudden rushes the tail fin is used, but lizard fishes do not often swim when at leisure, preferring to creep about on the bottom on their very large pelvic fins. The pectorals are held out as wings and are probably used as planing devices in their sudden rushes after prey."

Like the Synodontidae and other benthic myctophoids, the Bathypteroidae are without a swimbladder. Having a firmly ossified skeleton and a well-developed muscular system, they must be denser than their surroundings. And as Houot & Willm (1955) first observed, *Benthosaurus* actually rests on the bottom, supported by its elongated pelvic and caudal rays, which form a tripod.

These supporting rays have a special structure. In the Bathypteroidae the two lowermost, principal caudal rays, which may be much prolonged, are stiffened through being composed of short, closely interlocking, lepidotrichia, these elements being much shorter than those of the other caudal rays. The outermost 2 (or 3) rays of each pelvic fin are also made of very short segments. The same kind of fin-ray modification occurs in the Synodontidae. The two lowermost principal caudal rays are usually comprised of shortened lepidotrichia and certain of the outer pelvic rays also have this special structure (in *Trachinocephalus myops*, the outer 5 pelvic rays ; in *Synodus* the outer 4 or 5 rays and in *Saurida* the outer 2 pelvic rays.

All three " legs " of this fin-tripod are thus specially modified, presumably to support the weight of the resting or creeping fish. The other significant feature is that the insertions of the pelvic fins are definitely in advance of the centre of gravity. The tripod rest is thus quite stable, which would not be so if the pelvics were inserted further back along the abdomen (in a typically " abdominal " setting). The forward migration of the pelvic fins would thus seem to be simply related to the formation of a stable undercarriage.

It is clear that the lizard-fishes get a quick take-off from this undercarriage, while observers have seen *Benthosaurus* dart forward from a resting position. Perhaps the raising of the body above the substratum also enhances sensory appreciation of the immediate environment. If, for instance, a fish is flattened against sand or ooze the lower parts of the lateral line system of the head and of the visual field are out of action. The tips of the fin-ray tripod may also give tactile information of local movements of invertebrate food in the deposits.

The other benthic myctophoids, the Aulopidae, Chlorophthalmidae, Ipnopidae and Bathysauridae have also lost the swimbladder. Again, certain of the outer pelvic rays and (usually) the lowermost principal caudal rays are relatively stout and composed of short segments. (In *Aulopus filamentosus* and *Latropiscus purpurissatus* the outer 4 pelvic rays and the 2 lowest caudal rays have this special structure. In *Chlorophthalmus agassizii* and *C. nigripinnis* this applies to the outer 2 or 3 pelvic rays and the lowermost caudal ray, but in *C. punctatus* no single ray of these fins is so differentiated. Concerning *Ipnops murrayi* and *Bathysaurus ferox*, the modification is confined to the pelvic fins, to the outer 3 pelvic rays in the former and to the outer 2 rays in the latter.) Lastly, the pelvic fins of all these fishes are inserted in advance of the centre of gravity.

These fin features are surely close enough to those of lizard-fishes and bathypteroids to suggest that the fishes of the above four families use their pelvic and caudal fins as a mobile tripod-undercarriage.[1] There is no observational evidence to support this view, and indeed, little is known of the biology of these fishes. But the close structural congruence of fin form, to which may be added the common possession of a well-shaped muscular body ending in a forked tail fin, are features suggestive of a darting, synodontid-like habit (based on a " tripod " rest, allowing of a quick take-off.

---

[1] It is interesting that the one crossopterygian fish (*Laugia grönlandica*, Stensiö, 1932) with thoracic pelvic fins has specially modified pelvic rays. Like the iniomous fishes described above, some of the pelvic rays are much stouter and composed of shorter lepidotrichia than the other fin rays. Did *Laugia* use its pelvic fins as supports and/or for walking along the bottom?

Aside from these features of fin pattern and form, the benthic myctophoids have few characters in common. Evidently they are not closely related, except perhaps for the Synodontidae and Bathysauridae. In fact, the Chlorophthalmidae are more closely allied to a pelagic family, the Scopelosauridae (Marshall, in the press), than to any of the benthic groups. The similar pelvic and caudal characters of these groups may thus be due to (adaptive) convergent evolution rather than to inheritance from a common ancestor.

As in the Synodontidae, the pelvic fins of the Ctenothrissidae are considerably larger than the pectorals and composed of much stouter rays. Woodward (1903) described the pelvic fins of *Ctenothrissa radians* as follows : " Each of them consists of seven or eight very stout rays all articulated and all, except for the foremost, finely divided in their distal half." If these fins were part of a " percoid " type of braking system, they seem disproportionately large for such a function. But their robust structure may well point to their use as supports when the fish was resting on the bottom. The fact that they have a forward, thoracic setting could then be related to the requirement of an insertion anterior to the centre of gravity. In deep bodied, large-headed fishes, such as *Ctenothrissa* spp., this centre comes close behind the bases of the pectoral fins. In fact, the deeper the body the nearer to the head will be the point of balance. To take an apt example, comparison of *Aulopus filamentosus* with *Latropiscus purpurissatus* reveals that in the former, which is the slimmer bodied, the insertions of the pelvic fins are appreciably behind those of the pectorals. In the deeper bodied *Latropiscus* the pelvics originate just behind the vertical level of the pectoral bases.

Are the adults of *Macristium chavesi* also bottom-living fishes that use their long pelvic fins as two legs of a tripod undercarriage? In the *Discovery* specimen there is no sign of a swimbladder, the lack of which is a particular feature of fishes that spend most of their adult life actually resting on the bottom.

To return to our original question, the foregoing discussion might suggest that the resemblance between the fin patterns of *Macristium* and the ctenothrissids are due to convergent evolution. But our functional analysis of fishes with synodontid-like habits of resting on the bottom simply refers to the paired fins. Nevertheless the striking resemblances between the fin patterns and fin-ray numbers of *Latropiscus purpurissatus* and *Bathysaurus ferox* shows what " Nature can do " by way of convergence. Yet the aulopids and *Bathysaurus* are quite unlike in head structure, whereas *Macristium* and the ctenothrissids have a cluster of head characters in common. The pattern of gill cover bones might, of course, be simply correlated with the forwardly inclined suspension of comparatively small jaws (see p. 365). If so, the convergent features of these fishes would reside in both fin and gill cover pattern.

Against such considerations must be set the correspondence in number of branchiostegal rays and the fact that the *Macristium*-ctenothrissoid fin pattern is unique within the order Isospondyli (p. 364). Furthermore, no single feature or combination of features, precludes the consideration of *Macristium* as a ctenothrissoid fish. The absence of supramaxillae in *Macristium* seems the most outstanding difference, but these bones may be quite late in ossifying (p. 366). Certainly, the paddle-shaped bone that appears to be the maxilla has a most unusual shape if it is going to be no more than a maxilla.

In conclusion, these problems can only be resolved when an adult *Macristium* becomes available. We shall then know whether each maxilla carries two supramaxillae and whether the parietals meet in the middle line. If the answers are in the affirmative it would seem that *Macristium* can be regarded as a modern survivor of the ctenothrissoid fishes. Meantime the purpose of this paper is to suggest that this outcome is at least possible, perhaps even probable.

ACKNOWLEDGEMENTS. Thanks are due to Dr. N. A. Mackintosh for placing this material at our disposal.

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THE DISTRIBUTION OF PELAGIC POLYCHAETES ACROSS THE NORTH PACIFIC OCEAN

NORMAN TEBBLE

23 FEB 1962
PRESENTED.

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Pp. 371–492 ; 55 *Text-figures*

BRITISH MUSEUM

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THE DISTRIBUTION OF PELAGIC POLYCHAETES ACROSS THE NORTH PACIFIC OCEAN

By NORMAN TEBBLE

THE principal purpose of this report is to examine the extent to which pelagic polychaetes are restricted in their distribution in the North Pacific Ocean at the northern boundary of the Sub-Tropical Zone and the southern boundary of the Sub-Arctic Zone. Previously reported collections from this region have been confined to material from small areas, or from a few stations scattered over the ocean. The essential requirements for such a study, abundant samples from stations made across the major hydrological boundaries of the region, were provided by the collections of the University of California, Scripps Institution of Oceanography, La Jolla, California. It is principally on an examination of these collections that this study is based.

It is a pleasure to record my gratitude to the Royal Society of London for the award of the John Murray Travelling Studentship in 1958 which made possible my visit to the Scripps Institution of Oceanography, and also to that Institution for providing facilities during the first year of study. To Dr. Martin Johnson, Professor of Marine Biology at La Jolla, I am particularly grateful for inviting me to make this report, and for encouragement and criticism throughout its preparation ; other colleagues at Scripps, including Dr. J. A. McGowan and Dr. L. Berner, also provided invaluable advice. Miss Dorothy Tyler was responsible for sorting the plankton samples, and, for her sedulous work, I am very much indebted. Mr. Bob Winsett has prepared the drawings of complete specimens (Text-figs. 4–6, 13, 19, 21–23) and it is a pleasure to pay tribute to his artistic ability. Dr. Warren Wooster and Mr. Bruce Taft provided guidance in the interpretation of hydrological data. At the British Museum (Natural History) the Keeper of Zoology, Dr. F. C. Fraser, has given continual support and encouragement to this work and Miss A. C. Edwards has been very helpful in the preparation of drawings and charts.

MATERIAL AND METHODS

The plankton samples examined in this report were collected by ships of the Scripps Institution of Oceanography on the Trans-Pacific Expedition, 1953 ; Northern Holiday Expedition, 1951 ; Chinook Expedition, 1956 ; and by the Pacific Oceanic Fisheries Investigations of the U.S. Fish and Wild Life Service, Honolulu, *Hugh M. Smith* Cruise 30, 1955. The positions of the stations at which the samples were collected are shown in Text-fig. 1, and the number of samples examined tabulated according to Expedition, Zoogeographical location and depth in Table I.

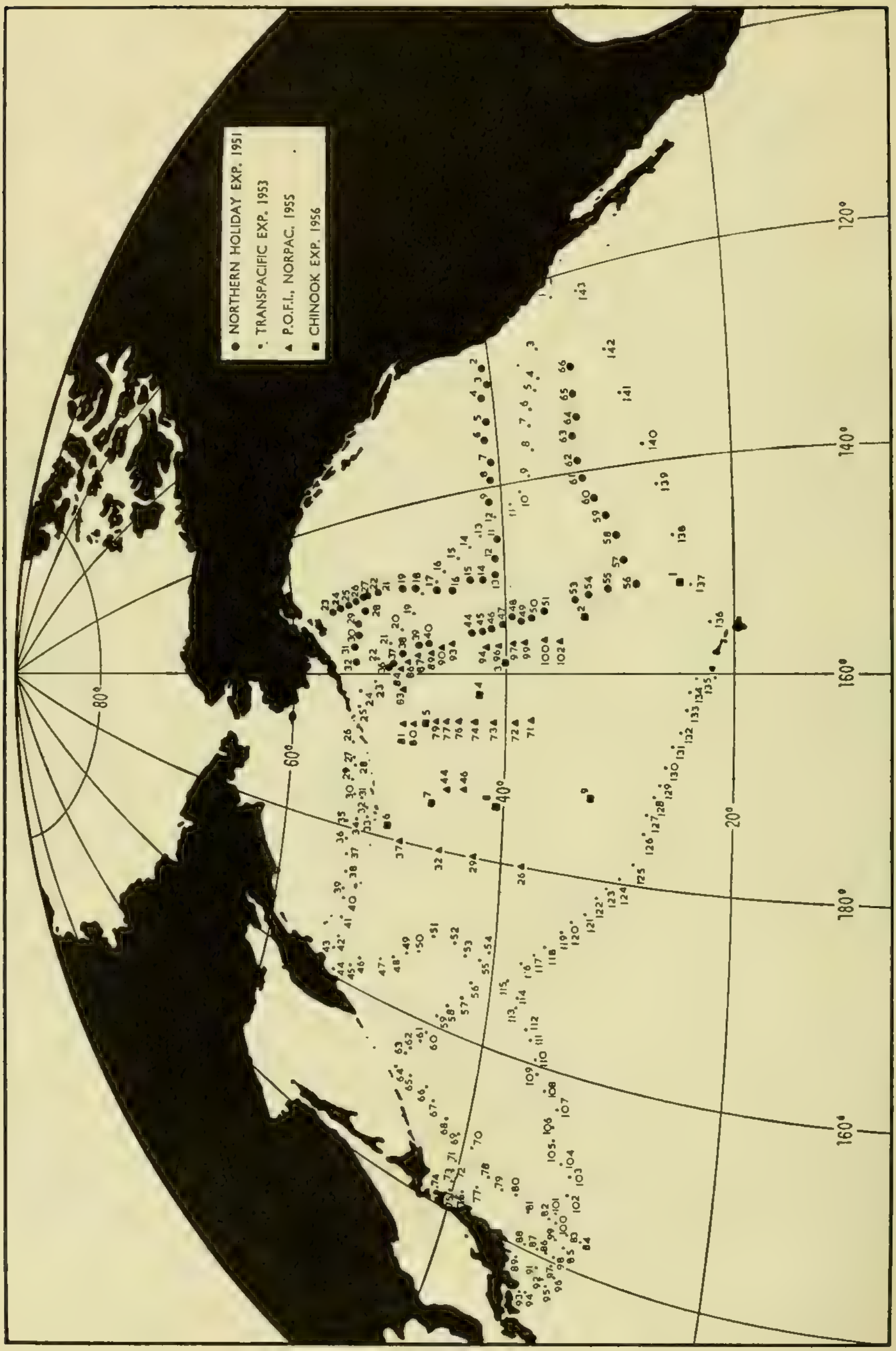
● NORTHERN HOLIDAY EXP. 1951
· TRANSPACIFIC EXP. 1953
▲ P.O.F.I., NORPAC. 1955
■ CHINOOK EXP. 1956
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 1. Chart showing the positions of stations from which plankton samples have been examined.

TABLE I.—*Number of Samples Examined, According to Expedition, Zoogeographical Location and Depth*

Depth of tow (metres)	Sub-Tropical Zone	Transition Zone	Sub-Arctic Zone	Totals
TRANS-PACIFIC EXP.—				
190–0	72	10	52	
Between 530 and 190–0	38	3	11	
Between 1,280 and 530–0	9	2	6	
150–35	0	0	2	
385–75	38	7	30	
720–210 (Mainly 500–300)	18	3	13	
680–495	3	2	2	
850–680	2	0	0	
1,175–525	0	0	1	
Subtotals	180	27	117	324
NORTHERN HOLIDAY EXP.—				
Between 227 and 118–0	31	6	18	55
P.O.F.I. *H. M. S.* CRUISE 30—				
145–0	13	9	6	28
CHINOOK EXP.—				
Between 130 and 85–0	5	4	3	9
Totals	229	45	142	416

These samples represent the material which was sorted for pelagic polychaetes. Both negative and positive results from them are recorded on the distribution maps for the various species except for the maps recording quantitative distribution on which *Hugh M. Smith* cruise 30 results have not been plotted. No details of the amount of water filtered by each net are available for this cruise but this information is available for the other expeditions. Details of number of specimens of all species collected are tabulated in Appendix I, Tables I and II.

Except for the University of Washington collections, which were made with a mid-water trawl, all the samples were collected with 1-metre nets, which have a mesh of 0·65 mm. (29 to the inch) of 30 xxx, silkgrit gauze. This net appears to be most efficient for catching pelagic polychaetes, the majority of which fall within the 5 to 35 mm. size range. Use of this net helps to explain the large number of records made here and by Dales (1957) for species not previously known to occur in abundance. For example, in the South Atlantic collections of *Discovery* from the Tropical and Sub-Tropical Zones (Tebble, 1960), when 1-metre nets were comparatively rarely used and the TYF (with a 2-metre frame and 10–12 meshes to the inch) normally in operation, no catches of *Sagitella kowalewskii* were reported, although it is known to occur there (Friedrich, 1950). In the North Pacific this species has been collected with persistant regularity (Text-fig. 48). On the other hand there were many more records for the larger *T. nisseni* (up to 70 mm. in length) from *Discovery* collections, than from the North Pacific, because it was more easily caught by the larger net. Nevertheless, for most pelagic polychaetes measuring less than 35 m. long, the 1-metre net appears to provide a better chance of catching a larger number of species.

This question of net efficiency is a debatable point (it is clearly associated with comparative abundance, type of tow, etc.) yet its importance cannot be overlooked, and the success of the Scripps Institution's Expeditions and of CCOFI (Dales, 1957) in catching pelagic polychaetes with the 1-metre net warrants comment.

Details of how the nets were operated on the Trans-Pacific Expedition, in both open and closed tows, have been given by McGowan (1960).

The collections made by the University of Washington were kindly provided by Mr. William Aron whose research is supported by the National Science Foundation and by the Office of Naval Research, Contract 477 (10). The mesh size of the nets used in making these collections and the method of towing is such that the smaller beasts are bound to be squeezed out of the net. For this reason I have not plotted the negative records from this collection on the distribution maps in this paper. The positive records, however, have been plotted, and details are tabulated in Appendix I, Table III.

Hereafter the report is divided into four sections :

(1) *Hydrological Environment*, a brief account only ; the reader is referred to the relevant parts of Chapter XV, in Sverdrup *et al.*, 1946 for greater detail ;

(2) *Systematic Account* ;

(3) *Distribution* ;

(4) *Zoogeographical Review*, in which the principal features of the distribution are examined in relation to other oceans and other animal groups, etc.

HYDROLOGICAL ENVIRONMENT

The collections reported here were made principally in the two major water masses of the North Pacific Ocean, the Sub-Arctic water mass in the Sub-Arctic Zone and the North Pacific Central water mass in the Sub-Tropical Zone. Between these there is generally a broad belt of water with intermediate hydrological characteristics in the Transition Zone from which samples have also been examined (Text-fig. 3).

The term Sub-Arctic water should be strictly applied only to the top 1,000 m. of water north of 45° N. (Sverdrup *et al.*, 1946) and it is principally in this sense that the term is used in this paper. No attempt is made here to interpret, in detail, distribution along the western coast of the U.S.A., between 48° N., and 23° N., where a southward flow of modified Sub-Arctic water, the California Current, exists prior to converging with Equatorial water.[1]

The hydrological data obtained on the Trans-Pacific Expedition has been inter-

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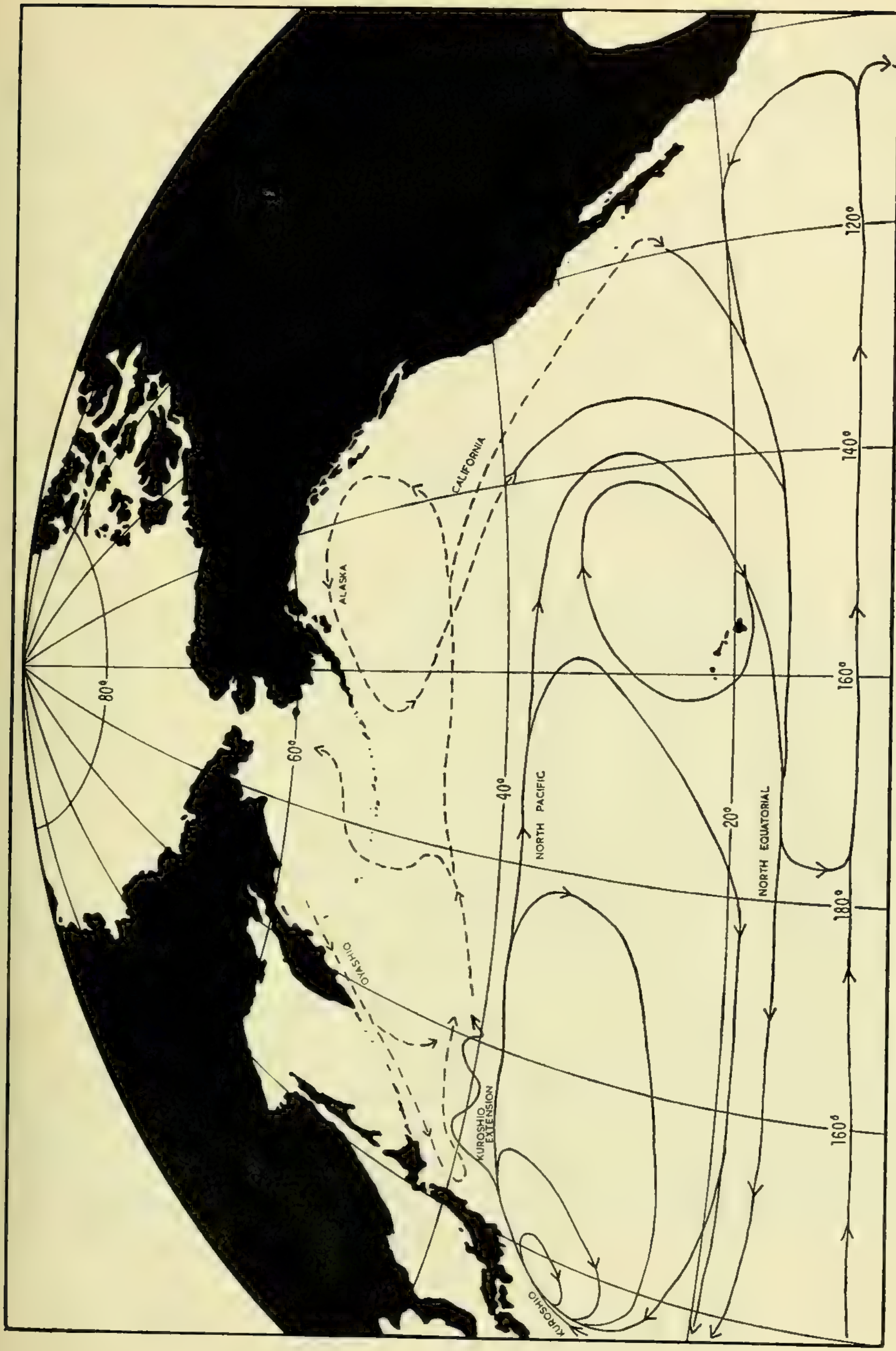
[1] Dales (1957) has reported on the distribution of pelagic polychaetes in the California Current (1949-50) within 75 metres of the surface : his data will be referred to here in terms of general oceanic distribution only.


80°
60°
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120°
140°
160°
180°
160°
ALASKA
CALIFORNIA
NORTH PACIFIC
NORTH EQUATORIAL
OYASHIO
KUROSHIO EXTENSION
KUROSHIO

FIG. 2. Chart showing the approximate direction of the transport of water in the North Pacific above 1,500 m. (after Sverdrup *et al.*, 1946, fig. 205).

preted by Warren Wooster and Bruce Taft and the T/S diagram (Text-fig. 3) prepared by them. This diagram differs from that in Sverdrup *et al.* (1946, fig. 209B) in that no differentiation has been made between Eastern and Western North Pacific Central water. In a schematic sense, however, it does indicate clearly the characteristics of the Sub-Arctic water mass, the broad belt of Transition water and the North Pacific Central water as sampled in 1953 by the Trans-Pacific Expedition.

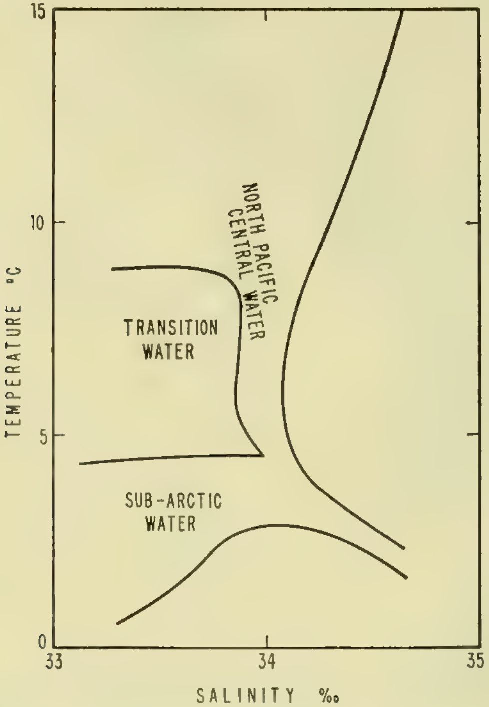

Fig. 3. Temperature/salinity diagram for the North Pacific Ocean from data obtained by the Trans-Pacific Expedition, 1953.

From the T/S diagram Wooster and Taft have interpreted the positions of stations from which samples have been examined ; these positions have been plotted on all distribution maps. Normally positions of the stations in relation to the water masses are comparatively clear but, in the region off the north-east coast of Japan, where the warm Kurushio current meets the cold Oyashio (Text-fig. 2), the conditions are more complicated. Thus Stations 71, 72, 73 and 78 were essentially Sub-Arctic in character but had a layer of Transition water at the surface, and Stations 74 and 77 Sub-Arctic below 450 metres but in North Pacific Central water above this depth.

SYSTEMATIC ACCOUNT

This section deals with descriptions of the species collected and with a re-examination of the taxonomic status of some of them. A short note on general distribution is appended to each description, but reference should be made to the section on Distribution (below, pp. 428–469) for a more detailed consideration of this aspect of the work.

Recent systematic analyses of pelagic polychaetes by Støp-Bowitz (1948), Dales (1957) and Tebble (1960) make repetition of lengthy lists of synonyms unnecessary. References to descriptions of species have therefore been restricted to these three works, original descriptions and Fauvel (1923) except where necessary. The spelling of specific names in these lists of synonyms follows that used in each particular reference.

The material collected by the research ships of the University of California has been deposited in the British Museum (Natural History) collections, Reg. No. 1960.6.1. 1–11,186, and the Scripps Institution of Oceanography, La Jolla, California; material collected by the Pacific Oceanic Fisheries Investigations in the Smithsonian Institution, Washington D.C., and by the University of Washington, is in the University Dept. of Oceanography, Seattle.

Family TOMOPTERIDAE

Exclusively pelagic. Prostomium with a pair of laterally directed antennae which together form its anterior border, a pair of nuchal organs and normally a pair of eyes. There may be two pairs of lateral processes just behind the eyes of which the anterior and smaller pair is often not present (the first pair of chaetigers) whereas the posterior pair is always present (the second pair of chaetigers). Parapodia are biramous and achaetous with notopodia and neuropodia modified into paddle-shaped pinnules. These pinnules may carry glands which have been given the following names: (*a*) chromophil glands, these are large glands which normally appear only in neuropodia and stain deeply with haematoxylin; (*b*) hyaline glands, small glands which occur in either notopodia or neuropodia, they may be pigmented or appear only as crystalline spots; they do not stain with haematoxylin; (*c*) rosette glands, very small glands which occur on the trunks of the parapodia or on notopodia and neuropodia, they do not stain with haematoxylin; (*d*) spur glands, these are small, normally subsidiary to the chromophil glands, and occur only on neuropodia, they stain with haematoxylin. Posteriorly the body may be prolonged into a tail, bearing rudimentary parapodia.

Genus ***TOMOPTERIS*** Eschscholtz, 1825

Notopodial and neuropodial pinnules always completely surrounding the parapodial trunk.

Type species. *Tomopteris onisciformis* Eschscholtz, 1825.

Type locality. South Seas (Pacific).

I have given elsewhere (Tebble, 1960) my reasons for not accepting the subgeneric division of *Tomopteris* into *Tomopteris* (*sensu stricto*) and *Johnstonella*.

TABLE II.—*In this Table the Presence* (×) *or Absence* (—) *of the More Important Diagnostic Characters in Some Species of* Tomopteris *is Indicated*

		Hyaline glands					Chromophil glands				
	First chaetigers	Apical	Dorsal	On most feet	On 3rd and 4th feet only	Rosette glands	Compact	Diffuse	With spur	Pinnules extend to body wall	Tai
T. planktonis	—	×	—	×	—	—	×	—	—	—	—
T. septentrionalis	—	—	×	×	—	—	—	×	—	—	—
T. ligulata	—	—	×	×	—	—	×	—	—	×	—
T. elegans	×	—	×	—	×	—	×	—	—	—	—
T. nisseni	—	×	—	×	—	—	×	—	—	—	×
T. krampi	×	×	—	×	—	—	×	—	—	—	×
T. apsteini	×	—	—	—	—	×	×	—	×	—	×
T. pacifica	×	—	—	—	—	×	×	—	—	—	×

* Of the species listed *T. krampi* was not present in the collections but was reported in the North Pacific from Monterey Bay by Dales (1955).

Tomopteris elegans Chun, 1887

(Text-fig. 4*a*, *b*)

Type locality. Canary Islands, 500–1,300 m.

Tomopteris elegans Chun, 1887, pp. 18–19, pl. 3, figs. 4–9.
Tomopteris (*Tomopteris*) *elegans:* Fauvel, 1923, p. 223, fig. 84, *b, c*.
Tomopteris (*Tomopteris*) *elegans:* Støp-Bowitz, 1948, pp. 46–48, fig. 33*a–b*.
Tomopteris elegans: Uschakov, 1957*a*, pp. 283–284, Chart 3, fig. 7*a–c*.
Tomopteris (*Tomopteris*) *elegans:* Dales, 1957, pp. 142–143, figs. 51a, 52a, 53.
Tomopteris elegans: Tebble, 1960, pp. 179–180, fig. 11, *a–c*; pp. 250–252, fig. 48.

DESCRIPTION. This species varies between 1·5 mm. in length for ten pairs of parapodia and 6·5 mm. for fifteen pairs, with most specimens having fourteen pairs. The anterior border of the antennae has a pronounced central indentation and there is a pair of pale brown eye spots on the prostomium. (These may not be well preserved.) The first pair of chaetigers is always present; the second pair varies in length but normally reaches to almost the total length of the body (though frequently broken off, as in the specimens shown in Text-fig. 4). Pigmented hyaline glands are present on the notopodial pinnules of the third and fourth parapodia only; they are absent from all other feet. Compact chromophil glands appear from the fourth neuropodial pinnule on all parapodia up to the end of the body; they are ventral in position just below the apex of the parapodial trunk. There is no tail in this species.

DISCUSSION. Dales (1957: 160) notes that *T. elegans* has, "Gonads present in the 3rd to 8th pairs of parapodia"; by gonads he must mean gonadial products, but I have never found these restricted to particular segments in this species. Text-fig. 4*a* shows them occurring in every foot from the first to the tenth and I have seen them in all and in only one[1].

---

[1] Dales uses this character to separate *T. elegans* from *T. kefersteini* Greeff, 1879, which he considers has "gonads present in the 3rd to 9th parapodia". In fact *T. kefersteini* has itself been described with gonads in all feet (Fauvel, 1923); and although a little-known species it can be distinguished from *T. elegans* by characters noted in its original description (Greeff, 1879).

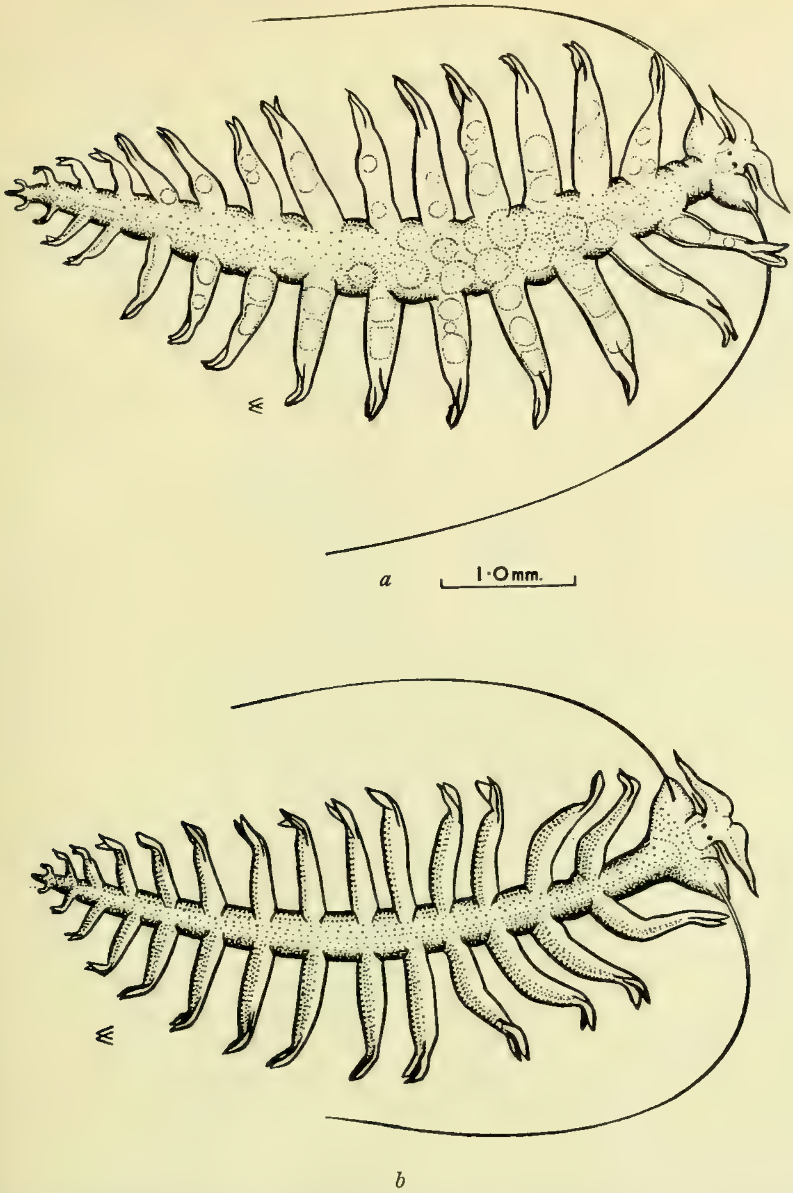

FIG. 4. *Tomopteris elegans :* (*a*) with and (*b*) without eggs in the body cavity. Both specimens are from Stn. 17A of the Trans-Pacific Expedition, and have had the tips of the second pair of chaetigers broken off.

General distribution. *T. elegans* is known only from Tropical and Sub-Tropical waters (see below, pp. 428–434).

Tomopteris septentrionalis Quatrefages, 1865

(Text-fig. 5)

Type locality. " . . . les mers du Danemark ".

Tomopteris septentrionalis Steenstrup, 1849, p. iv (*nomen nudum*).
Tomopteris septentrionalis Quatrefages, 1865, p. 229.
Tomopteris (*Tomopteris*) *septentrionalis*: Støp-Bowitz, 1948, pp. 49–51, figs. 36–37.
Tomopteris septentrionalis: Uschakov, 1957*a*, pp. 282–283, Chart 3.
Tomopteris (*Tomopteris*) *septentrionalis*: Dales, 1957, p. 145, figs. 51*f*, 52*g*, 54.
Tomopteris septentrionalis: Tebble, 1960, pp. 176–177, fig. 8*a*, *b*; pp. 228–231, figs. 32, 33.

Description. The specimens of this species collected vary in length between 1·5 mm. for twelve pairs of parapodia and 20–28 mm. for twenty to twenty-four pairs. The anterior border of the antennae has a prominent central indentation and there is a pair of eye spots on the prostomium. The first pair of chaetigers is never present; the second pair extends almost as far as the body length. The hyaline gland is normally clearly pigmented a red-brown, and appears dorsally on

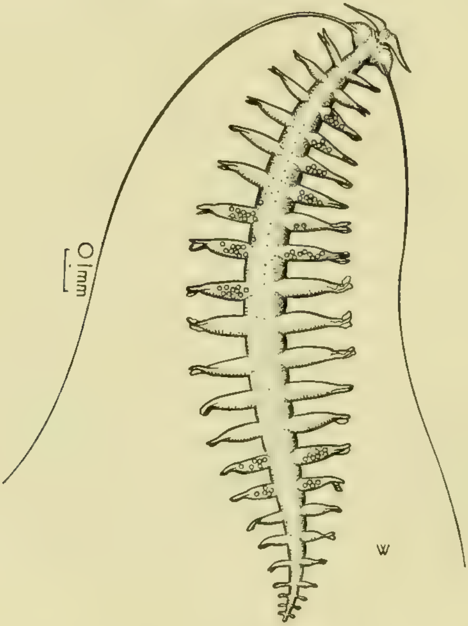

Fig. 5. *Tomopteris septentrionalis*: complete specimen from Stn. 1B of the Trans-Pacific Expedition.

the neuropodial pinnule from the first parapodia, although it may not be distinct on all feet. The chromophil gland appears first on the third pair of parapodia and subsequently on all feet ; it is not a compact gland but consists of a series of ramifying tubules situated between the ventral and apical surfaces. There is no tail in this species.

DISCUSSION. The largest specimens of *T. septentrionalis* from the South Atlantic (Tebble, 1960) are 15 mm. in length, much smaller than the largest reported here from the North Pacific, which are between 20 mm. and 28 mm., a similar size range to that reported by Uschakov (1955) and Berkeley and Berkeley (1957). In general these larger specimens appeared more often in the Sub-Arctic water mass than elsewhere, but more material from warmer waters will have to be examined before the possibility that the Sub-Arctic Zone harbours a distinct population can be sustained.

GENERAL DISTRIBUTION. *T. septentrionalis* has been reported from all explored water masses throughout the world (see below pp. 430–434).

Tomopteris planktonis Apstein, 1900

Original localities. In the Atlantic Ocean between Ascension Island and Brazil, Ascension Island and Cape Verde Islands and between Newfoundland and Iceland.

Tomopteris planktonis Apstein, 1900, p. 42, pl. 11, figs. 21, 22 and pl. 12.
Tomopteris (Tomopteris) planktonis : Fauvel, 1923, pp. 224–225, fig. 84, *d*.
Tomopteris (Tomopteris) planktonis : Støp-Bowitz, 1948, pp. 52–54 (in part), fig. 39.
Tomopteris (Tomopteris) cavallii : Dales, 1957, pp. 144–145, figs. 51*b*, 52*b*.
Tomopteris planktonis : Tebble, 1960, pp. 171–174, fig. 6, *a–f* ; pp. 228–231, fig. 31.

DESCRIPTION. The smallest specimens of this species in the collection measure 2 mm. in length for twelve pairs of parapodia and the largest 9 mm. for eighteen pairs. The anterior border of the antennae is entire and there is a pair of eyes on the prostomium. The first pair of chaetigers is never present. The second pair reaches to about two-thirds the length of the body. Small hyaline glands appear apically on the neuropodial pinnule of all parapodia but they are frequently indistinct. Compact chromophil glands appear on all neuropodial pinnules from the fourth, they are ventral in position and when fully developed extend right into the angle between the pinnule and the ramus. In some specimens there are tubules, like those which make up the chromophil gland, in the dorsal region of the neuropodium and ventral in the notopodium. Bands of brown pigment appear on some specimens either encircling the body or confined to the dorsal or ventral surfaces. There appears to be no particular pattern manifest in the occurrence of these. There is no tail in this species.

DISCUSSION. This material is identical with that reported from the California Current by Dales (1957) as *T. cavallii* ; this species differs from *T. planktonis* in having no hyaline glands but these are present in the material reported here, and by Dales which has been deposited in the British Museum (Natural History).

The appearance of chromophil gland tubules in a dorsal position in neuropodia and ventrally in notopodia in some specimens was noted by Dales (1957, as in *T.*

cavallii) and my observations confirm this. There is no regularity about the appearance of these tubules ; they appear on specimens from widely separated stations, and at one station some specimens may have them and some not. Bands of brown pigment have not, to my knowledge, previously been seen on *T. planktonis* ; these again appear to occur in no regular manner. The extent, and importance, of this variation may become more apparent when comprehensive collections to the south of the area now investigated have been examined.

GENERAL DISTRIBUTION. *T. planktonis* has been widely reported throughout the world from all explored water masses but in the North Pacific it has not been collected in the Sub-Arctic Zone (see below, pp. 434–435).

Tomopteris ligulata Rosa, 1908

Original localities. Atlantic Ocean, 22° N., 35° W., 33° S., 30° W. ; Pacific Ocean, 31° S., 84° W.

Tomopteris ligulata Rosa, 1908*a*, p. 1.
Tomopteris ligulata : Rosa, 1908*b*, pp. 302–304, pl. 12, figs. 18–19.
Tomopteris (*Tomopteris*) *ligulata :* Fauvel, 1923, p. 224, fig. 84*e*.
Tomopteris ligulata : Tebble, 1960, pp. 177–179, figs. 9, 10 ; p. 248, fig. 47.

DESCRIPTION. The smallest specimen of this species in the collection measures 2 mm. in length for twelve pairs of parapodia and the largest 7 mm. for eighteen pairs. The anterior border of the antennae is entire and there is a pair of eyes on the prostomium, these are normally distinct but on occasion may be difficult to see. There is no first pair of chaetigers, the second pair reaches to about two-thirds of the body length. The hyaline gland is distinctly pigmented—normally a red-brown and appears in a dorsal position from the third neuropodial pinnule up to the end of the body. The chromophil gland is compact and appears ventrally from the fourth neuropodial pinnule. The pinnules border the parapodia almost to the junction with the body wall. There is no tail in this species.

GENERAL DISTRIBUTION. This appears to be the first record of *T. ligulata* from the North Pacific Ocean (see below, pp. 437, 438). In the Atlantic Ocean it is known only from Tropical and Sub-Tropical waters.

Tomopteris nisseni Rosa, 1908

Type locality. Atlantic Ocean 20° S., 27° W.

Tomopteris Nisseni Rosa, 1908*a*, p. 1.
Tomopteris (*Tomopteris*) *Nisseni :* Rosa, 1908*b*, pp. 292–294.
Tomopteris (*Tomopteris*) *Nisseni :* Fauvel, 1923, p. 222, fig. 82*e*, *g*.
Tomopteris (*Tomopteris*) *Nisseni :* Støp-Bowitz, 1948, pp. 44–46, figs. 29–30.
Tomopteris nisseni : Tebble, 1960, pp. 180–181, pp. 246–248, fig. 46.

DESCRIPTION. All the specimens collected are in a poor condition of preservation, making examination difficult. In addition they are probably all young forms, the glands are not developed on all feet and the largest measures only 12 mm. in length for fourteen pairs of parapodia. Adult specimens of this species may measure up to 60 mm. in length. The antennae are long and thin and have a prominent central indentation. A first pair of chaetigers is never present ; the second pair is exceedingly long-reaching in young forms to four or five times the length of the body. Parapodial pinnules are reduced to a fringe bordering the rami. Apical hyaline glands appear first on the neuropodial pinnules of the third parapodia and in notopodia from about the eighth. Compact chromophil glands appear on the ventral part of the neuropodial pinnules in all parapodia from the fourth. A tail is present in this species but in most of the specimens examined here it has broken off.

DISCUSSION. There are no eye spots visible in any of these specimens ; this is either because they are juveniles, or because of the poor state of preservation. In well-preserved adult *T. nisseni* I would certainly expect a pair of eye spots to be present.

GENERAL DISTRIBUTION. In the Atlantic Ocean *T. nisseni* has been reported from all explored water masses except south of the Sub-Tropical Convergence in the South Atlantic ; in the North Pacific it has not been collected north of the Sub-Tropical Zone (see below pp. 437, 439).

Tomopteris apsteini Rosa, 1908

Type locality. Messina, Mediterranean Sea.

Tomopteris (Tomopteris) Apsteini Rosa, 1908*b*, pp. 288–292, pl. 12, figs. 10–13.
Tomopteris (Johnstonella) Apsteini : Fauvel, 1923, pp. 220–221, fig. 83, *a–d.*
Tomopteris (Johnstonella) Apsteini : Støp-Bowitz, 1948, pp. 39–42, figs. 26–27.
Tomopteris apsteini : Tebble, 1960, p. 183 ; p. 252, fig. 48.

DESCRIPTION. The smallest specimen of this species in the collection measures 8 mm. in length for nineteen pairs of parapodia and the largest 18 mm. also for nineteen pairs. The anterior border of the antennae carries a central indentation. There is a pair of eye spots on the prostomium. The first pair of chaetigers is present extending almost to the length of the antennae ; the second pair reaches to about two-thirds of the length of the body. Rosette glands appear on all parapodia ; on the first two there is one present near the ventral surface within the ramus ; thereafter one is present on all notopodial and neuropodial pinnules near the apex of the parapodial trunk. The characteristic " spur " glands may appear in the first neuropodia projecting prominently from the ventral border of the pinnules. They are always present from the second parapodia and from the third are associated with the large compact chromophil gland. A prominent tail is present normally carrying rudimentary parapodia.

GENERAL DISTRIBUTION. *T. apsteini* is known only from Tropical and Sub-Tropical waters (see below, pp. 437, 439).

Tomopteris pacifica Izuka, 1914

(Text-fig. 6)

Type locality. Misaki, Japan.

Tomopteris pacifica Izuka, 1914, pp. 11–12, figs. 1–4.
Tomopteris elegans Berkeley, 1924, pp. 5–6, pl. 1, figs. 1–2 (name preoccupied).
Tomopteris renata Berkeley, 1930, pp. 11–12 (new name to replace *T. elegans* Berkeley, 1924).
Tomopteris renata : Berkeley & Berkeley, 1948, p. 26, figs. 31–32.
Tomopteris (Johnstonella) pacifica : Uschakov, 1955, p. 109.

Tomopteris (*Johnstonella*) *renata*: Uschakov, 1955, p. 110.
Tomopteris (*Johnstonella*) *pacifica*: Dales, 1955, p. 440.
Tomopteris (*Johnstonella*) *renata*: Uschakov, 1957*a*, p. 285, Chart 3.
Tomopteris (*Johnstonella*) *pacifica*: Uschakov, 1957*a*, pp. 285–286, Chart 3.
Tomopteris (*Johnstonella*) *pacifica*: Dales, 1957, p. 141, fig. 51*e*, fig. 52*f*.
Tomopteris (*Johnstonella*) *renata*: Berkeley & Berkeley, 1957, p. 576.
Tomopteris (*Johnstonella*) *renata*: Berkeley & Berkeley, 1960, p. 791.

DESCRIPTION. This species measures between 8 mm. long for fourteen pairs of parapodia and 50 mm. for twenty-four pairs[1]. The antennae are long and thin and carry a central indentation. There is a pair of black eye spots on the prostomium. The first pair of chaetigers is normally present but may be broken off; the stumps, however, are always visible on the ventral surface, just beside the inner edge of the nuchal lobes. The second pair of chaetigers reaches to about two-thirds of the body length. Rosette glands appear on all parapodia; on the first two they are within the parapodial trunk thereafter on the pinnules immediately ventral to the ramus in the notopodium and dorsal in the neuropodium. Chromophil

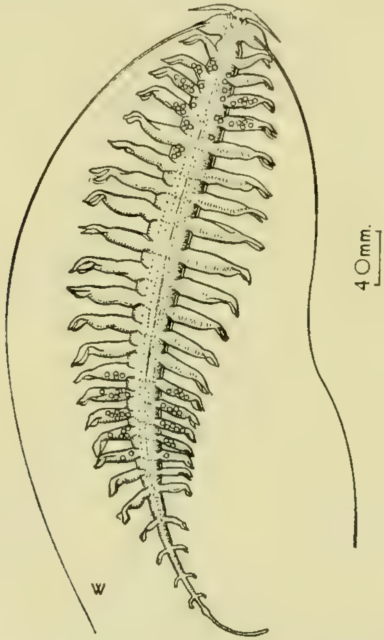

FIG. 6. *Tomopteris pacifica*: specimen from Stn. 46B of the Trans-Pacific Expedition, the first pair of chaetigers has been lost.

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[1] One very poorly preserved specimen from Northern Holiday Expedition Station 23, which could be *T. pacifica* measures 135 mm. in length. This identification, however, cannot be confirmed and has neither been plotted on a chart nor recorded in the appendices of this report.

glands are compact and appear ventrally on the neuropodia of all parapodia from the third backwards. All glands, except the rosettes on the first two parapodia, are always well preserved and clearly visible. A prominent tail with rudimentary parapodia is normally present though it may be broken off.

Discussion. After examining co-type material of *T. renata* Berkeley in the collections of the B.M. (N.H.) (Reg. No. 1938.11.29.6–8) I have no doubt that this species is identical with *T. pacifica*. Berkeley & Berkeley (1957 and 1960) reject the possibility of such synonymy mainly on the grounds that *T. renata* is much the larger, with an abrupt transition from the body to the tail region. I can find no evidence for supporting such a conclusion. The principal difficulty in accepting these two species as identical results from the ease with which the first pair of chaetigers becomes detached from the body. These are almost certainly lost accidentally and not, as suggested by Berkeley (1930), naturally, in the course of the life history of the animal. There are no observations on living tomopterids which substantiate Berkeley's suggestion. Of the specimens examined in this survey over half have lost the first chaetigers and have only the stumps remaining. At some stations some specimens have retained them and others lost them, and at Trans-Pacific Station 50B, the chaetiger is present on one side and missing on the other. In all other characters these specimens are identical with those in which the first chaetigers are present. There is no doubt that identification is difficult when situations of this type arise and confusion between *T. pacifica* and *T. nisseni* and *T. kempi* is possible in this present case.

Text-fig. 6, of *T. pacifica*, has been prepared from a specimen which has lost the first pair of chaetigers.

General distribution. From the evidence obtained in this survey *T. pacifica* appears to be restricted to the Sub-Arctic water mass in the North Pacific Ocean (see below, pp. 434–437). The fact that it was first recorded from Misaki, just outside Tokyo Bay, with a number of other species which are certainly not Sub-Arctic forms, is also discussed below, p. 437.

Family ALCIOPIDAE

Exclusively pelagic. Body normally elongate with numerous segments: exceptionally short and wide with comparatively few segments. Prostomium small with two very large eyes and four, five or six antennae. There are three, four or five pairs of tentacular cirri. Proboscis eversible, with long terminal horns and/or short papillae. Uniramous parapodia, with simple and/or compound chaetae, often with pigmented segmental glands. In mature females some anterior dorsal cirri may be modified into receptacula seminis. Anal cirri present.

Table III below has been prepared to show the principal diagnostic characters of the parapodia which are used in separating genera in the Alciopidae.

Some authors, in particular Dales (1957), have used the angle subtended by the axes of the eyes as a character of value in separating species; in no specimen have I found evidence to support such use. It appears reasonable to assume that a character of this type will vary considerably with the method of fixation of the

TABLE III

Acicular chaetae	Absent	Absent	Simple	Simple	Compound
Capillary chaetae	Simple	Compound	Simple	Compound	Compound
Number of cirriform pedal appendages					
Nil	*Naiades*	*Torrea**	*Alciopina**	*Plotohelmis*	Not known
One	*Watelio**	*Vanadis*	*Krohnia*	*Rhynchonerella*	
Two	*Alciopa**	Not known	Not known	Not known	Not known

* Not reported here.

specimens. Of the Alciopidae reported here only *Naiades cantrainii* and *Rhynchonerella angelini* are normally complete when collected, the remaining species being almost always broken into fragments. In identifying fragments it is generally necessary to have at least the head and anterior parapodia to make a reliable determination. With two species, however, *Vanadis longissima* and *Krohnia lepidota*, the body is characterized by an ornamentation which allows a specific determination to be made with some certainty, even when the head is missing. It will be appreciated, however, that identification of fragments is an unsatisfactory state of affairs, although it is one which workers on polychaetes have to deal with frequently. In the Appendices the presence or absence of alciopid fragments has been noted as an indication of the occurrence of this family even when species were not identifiable. The zoogeographical importance of these results is discussed below, p. 440.

Genus ***NAIADES*** Delle Chiaje, 1830

Body elongate. Prostomium with five antennae. Three pairs of tentacular cirri. Proboscis bell-shaped with two short terminal lobes between which are small papillae. Parapodia with simple chaetae only ; the pedal lobe is without an appendage.

Type species. *Naiades cantrainii* Delle Chiaje, 1830.

Type locality. Naples.

Naiades cantrainii Delle Chiaje, 1830

Naiades cantrainii Delle Chiaje, 1830, pl. 82, figs. 14, 18, 21.
Alciopa cantrainii : Izuka, 1914, pp. 2–3, pl. 1, fig. 9.
Alciopa cantrainii : Fauvel, 1923, pp. 203–204, fig. 76.
Alciopa distorta Treadwell, 1943, p. 35, pl. 1, figs. 16, 17 ; pl. 11, fig. 18.
Naiades cantrainii : Støp-Bowitz, 1948, pp. 24–25, figs. 15–16.
Naiades cantrainii : Dales, 1957, pp. 113–115, figs. 18–20.
Naiades cantrainii : Tebble, 1960, p. 184, p. 257, fig. 51.

DESCRIPTION. Complete specimens of this species may measure up to 110 mm. in length. The body is sharply terminated anteriorly, the eyes projecting forward prominently with the small prostomium between them. There are two pairs of antennae on the anterior edge of the prostomium and an unpaired median antenna on the dorsal surface between the eyes; the latter is in fact a crest with a free anterior edge. There is one pair of tentacular cirri on each of three successive segments behind the head; the most anterior of these is very long, the posterior two minute. The first three pairs of parapodia are reduced, with no chaetae but with aciculae; in mature females the cirri of the second pair are modified as receptacular seminis. The remaining parapodia, up to the end of the body, each have a large foliaceous dorsal cirrus, a slightly smaller ventral cirrus, a prominent projecting acicula, long simple capillary chaetae and a strongly pigmented dorsal segmental gland.

DISCUSSION. I have examined the type specimen of *Alciopa distorta* Treadwell, 1943, in the Smithsonian Institution, No. 20084, and it is identical with *N. cantrainii*.

GENERAL DISTRIBUTION. *N. cantrainii* is known only from Tropical and Sub-Tropical waters (see below, pp. 440–441).

Genus ***VANADIS*** Claparède, 1870

Body elongate. Prostomium with two large eyes and with four, five or six antennae. There are three to five pairs of tentacular cirri. Parapodia with long compound chaetae; pedal lobe with terminal appendage. Proboscis with terminal horns and/or papillae.

Type species. *Vanadis formosa* Claparède, 1870.

Type locality. Gulf of Naples.[1]

KEY TO SPECIES OF *Vanadis*

1. With six antennae (Text-fig. 9) . . . . ***V. tagensis***
–. With four or five antennae 2
2. With four antennae (Text-fig. 7) . . . . ***V. minuta***
–. With five antennae (Text-fig. 8) 3
3. Proboscis terminated by twelve equal small papillae . . . . . ***V. longissima***
–. Proboscis terminated by two long horns and a varying number of small papillae . 4
4. Parapodia well developed and with chaetae from the third foot posteriorly ***V. formosa***
–. Parapodia well developed and with chaetae from the seventh to tenth feet posteriorly ***V. crystallina***

Vanadis formosa Claparède, 1870

Vanadis formosa Claparède, 1870, pp. 480–484, pl. 10, fig. 3.
Vanadis formosa: Fauvel, 1923, pp. 305–306, fig. 77, *a–c*.
Vanadis formosa: Treadwell, 1943, p. 36, pl. II, figs. 23–24.
Vanadis formosa: Støp-Bowitz, 1948, pp. 25–26, fig. 17, Chart 18.
Vanadis formosa: Dales, 1957, p. 117, figs. 21–24.
Vanadis formosa: Tebble, 1960, pp. 185–186; pp. 252–255, fig. 49.

DESCRIPTION. No complete specimens of this species were collected; the largest head-fragment measures 73 mm. long for seventy-two chaetigers but most pieces

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[1] Not the Island of Formosa (Taiwan) as in Dales (1957, p. 117, and fig. 63).

are less than 20 mm. in length. Wesenberg-Lung (1939) reports complete specimens up to 300 mm. long from the Mediterranean. All five antennae are small, the dorsal and ventral pairs on the anterior edge of the prostomium and the unpaired in the median line between the large eyes. The proboscis carries two long terminal horns each with a pair of basal ailerons continuous with rows of four to six papillae. There are three pairs of tentacular cirri, one on each of successive segments behind the head; the first pair is the longest and joined by bulbous basal ceratophores continuous under the ventral surface; the posterior pairs are equal in length and project out about half the distance of the anterior pair. In mature females the first two pairs of parapodia are reduced, with the dorsal cirri modified as receptacula seminis. In the male these parapodia are reduced but never modified. In both sexes, all parapodia from the third are well developed, with large foliaceous dorsal and smaller ventral cirri, with pedal mamelon and projecting acicula, and with cirriform appendage and compound chaetae with short terminal articles. Darkly pigmented segmental glands appear on each foot after the first three, except in mature females when they may appear in the first two modified parapodia.

GENERAL DISTRIBUTION. *V. formosa* is known only from Tropical and Sub-Tropical waters (see below, pp. 442, 447).

Vanadis crystallina Greeff, 1876

Type locality. Gulf of Naples.

Vanadis crystallina Greeff, 1876, pp. 68–69, pl. 4, figs. 35–39.
Vanadis crystallina: Fauvel, 1923, pp. 206–207, fig. 77, *d*, *e*.
Vanadis crystallina: Støp-Bowitz, 1948, pp. 27–29, figs. 19–20.
Vanadis crystallina: Dales, 1957, pp. 118–119, figs. 25–28.
Vanadis crystallina: Tebble, 1960, pp. 186–187, pp. 252–255.

DESCRIPTION. No complete specimens of this species were collected; the longest head-fragment is only 9 mm. long for twenty-five pairs of parapodia, but in *Discovery* collections from the South Atlantic (Tebble, 1960) a complete specimen was 143 mm. in length. *V. crystallina* differs from *V. formosa* in having the first seven to ten pairs of parapodia rudimentary, with no chaetae and only very small cirri; in *V. formosa* fully developed parapodia are present from the third foot.

GENERAL DISTRIBUTION. *V. crystallina* is known only from Tropical and Sub-Tropical waters (see below, pp. 442, 445).

Vanadis minuta Treadwell, 1906

(Text-fig. 7)

Type locality. Off Hawaii.

Vanadis minuta Treadwell, 1906, pp. 1158–1159, figs. 25–278.
nec. *Vanadis fusca-punctata* Treadwell, 1906, pp. 1159–1160, figs. 29–31.
Vanadis minuta: Dales, 1957, pp. 119–121, figs. 28–30.

Description. No complete specimens of this species were collected; the longest head-fragment is 15 mm. in length. Treadwell's original material does not appear to have been complete, the first twenty-one segments measuring 8 mm. The proboscis has two long terminal processes, each carrying a pair of basal ailerons between which there are no papillae. There are three pairs of small tentacular cirri, one on each of successive segments behind the head; the first of these pairs is the largest and joined ventrally by basal ceratophores; the second and third are equal in size. There are only four antennae, all on the anterior border of the prostomium arranged in dorsal and ventral pairs; of these the ventral pair is sharply pointed and noticeably the longer, being always at least twice as long as the blunt dorsal pair. No median unpaired antenna is present in this species: on the top of the prostomium, between the eyes (where the unpaired antenna is present in all other species of *Vanadis*) there is a pronounced crest but this cannot be called an antenna. The anterior seven pairs of parapodia are achaetous with very small cirri; thereafter parapodia are fully developed; chaetae are long and compound, cirri ovate, and the pedal lobe carries a cirriform appendage. In mature females the dorsal cirri of the second parapodia are modified as receptacula seminis. None of the specimens examined has the pigmented segmental glands preserved sufficiently well to allow accurate examination.

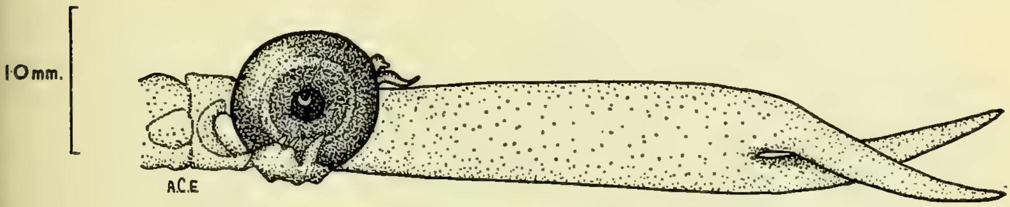

Fig. 7. *Vanadis minuta*: lateral view of head and extruded proboscis of specimen from Stn. 63 of the Northern Holiday Expedition.

Discussion. Dales (1957) was the first to record *V. minuta* after its original discovery; I have examined some of his specimens in the B.M. (N.H.) collections, and they are identical in all respects with those described here including having four antennae. In suggesting however, that *V. fusca-punctata* is synonymous with *V. minuta*, both he and Treadwell (1943) allow for the possibility that the latter species has a fifth unpaired median antenna as Treadwell's (1906) drawing of the type of *V. fusca-punctata* clearly shows this organ present, and his description mentions it. There is no precedent for suggesting any species of Alciopidae has a variable number of antennae; no work on the life history of any species of the family suggests this as likely. Indeed it is a basic tenet of the systematic analysis of adult polychaetes, that the number of antennae within a species is constant.

General distribution. *V. minuta* is known only from the Pacific Ocean where it has been collected in Tropical and Sub-Tropical waters (see below, pp. 440–443).

Vanadis longissima (Levinsen), 1885

(Text-fig. 8)

Type locality. 26° 0′ N., 26° 0′ W.

Rhynchonerella longissima Levinsen, 1885, pp. 330–331, figs. 7–10.
Vanadis grandis Izuka, 1914, pp. 5–7, pl. 1, figs. 1–7.
Vanadis longissima: Fauvel, 1923, p. 207, figs. 77*f–g*.
Vanadis pacifica Uschakov, 1957*a*, pp. 275–277, Chart 2, fig. 4*a–d*.
Vanadis longissima: Dales, 1957, pp. 121–123, figs. 31–33.
Vanadis longissima: Tebble, 1960, pp. 187–188; p. 224, fig. 27.

DESCRIPTION. No complete specimens of this species were collected; the longest head-fragment measures 160 mm. in length. There are four anterior antennae, in dorsal and ventral pairs on the front edge of the prostomium and a median unpaired antenna between the large eyes; irregular black spots may be present on the eyes in some specimens. The proboscis carries twelve small terminal papillae. There are three pairs of tentacular cirri, one on each of successive segments behind the head; all are approximately equal in length, the foremost pair being joined ventrally by basal ceratophores. The first pair of parapodia is achaetous with small foliaceous dorsal cirri and minute ventral cirri. In mature females the dorsal cirri of the second and third parapodia are converted into darkly pigmented receptacula seminis. From the fourth chaetiger parapodia gradually increase in size to a constant width from about the tenth; pedal lobes project about twice as far as the dorsal cirri and carry a prominent cirriform appendage; dorsal cirri are foliaceous and ventral cirri conical; chaetae are long and compound. On specimens other than mature females the second and third parapodia are achaetous with small cirri. Pigmented segmental glands appear at irregular intervals along the body, variously grouped over two to eight segments, with the pigment often extending over the ventral and dorsal surface, giving a striped appearance to the specimens. The first group of pigmented glands may appear on any of the first ten parapodia.

DISCUSSION. In reporting on the *Discovery* collections (Tebble, 1960) from the South Atlantic I noted that *V. longissima* and *V. antarctica* could be separated with certainty only from complete specimens. Because no complete specimens have been found in the present survey it follows that, theoretically, none of the determinations of *V. longissima* made here can be absolutely certain. In the Atlantic, and Pacific Oceans however, *V. antarctica* has never been reported north of the Antarctic Convergence and it is reasonable to assume that in the North Pacific Sub-Tropical Zone the material examined is *V. longissima*.

I do not think that *V. pacifica* Uschakov (1957*a*) is a valid species. Uschakov separates it from *V. grandis* (= *V. longissima*) on a combination of the different number of tentacular cirri and poorly developed anterior parapodia. Because tentacular cirri are frequently lost, and chaetae may be missing, either accidentally, or through normal development, on anterior feet, it is easy to mistake parapodial cirri for tentacular cirri. This Izuka (1914) did in his original account of *V. grandis*, and has led Uschakov to establish *V. pacifica* as a separate species.

Specimens of *V. longissima* from five localities, Trans-Pacific Exp., Stns. 51A, 54A, and 56A, and *Hugh M. Smith* Cruise 30, Stns. 74 and 96 have irregular black spots on the eyes and surrounding areas. Stn. 51A is from the Transition Zone, and the other four stations are from close to the boundary separating it from the Sub-Tropical Zone[1] and although these records are few the presence of specimens with this unusual character (the first time it has been recorded) in and near the Transition Zone should be noted as possibly indicative of a distinct population inhabiting this region. It is shown below, p. 442, that the northern boundary of the Transition Zone is the northerly limit of the distribution of *V. longissima* in the North Pacific and it is of interest that at its southern limit in the South Atlantic at the Antarctic Convergence it meets the endemic antarctic form *Vanadis antarctica*, which it was suggested in Tebble (1960), may be a geographical race rather than a separate species. This suggestion may now be taken a little further. It is possible that, at the extremities of its range in higher latitudes, *V. longissima* has developed, or is developing, separate populations capable of establishing themselves in dis-

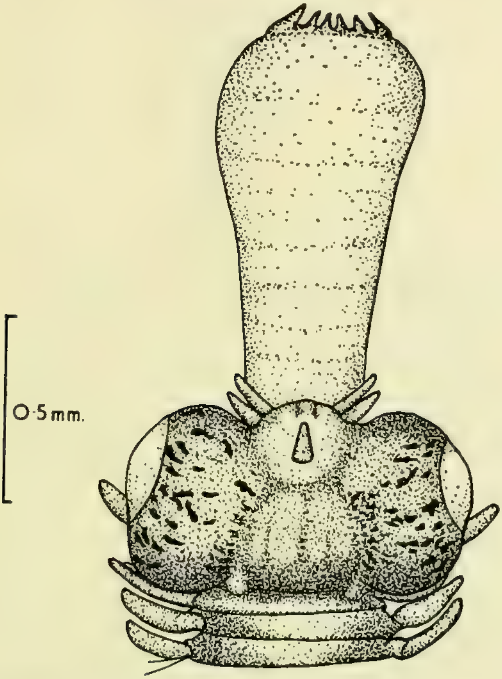

FIG. 8. *Vanadis longissima :* dorsal view of head and extruded proboscis, showing marking on the eyes ; specimen from Stn. 74, of *Hugh M. Smith* Cruise 30.

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[1] Specimens of *V. longissima* from Trans-Pacific Stns. 70E, 76A and *H. M. Smith* Cruise 30, Stn. 29 also near this boundary, are without heads.

tinctive hydrological environments. In the case of *V. longissima–V. antarctica* about the Antarctic Convergence, semi-sympatric speciation, involving ecological allopatry and genetical contiguity (Cain, 1954) may have taken place, whereas near the Transition Zone in the North Pacific *V. longissima* may be developing a physiological race.

GENERAL DISTRIBUTION. In the North Pacific and North Atlantic *V. longissima* has never been found in Arctic or Sub-Arctic waters (see below, p. 442); in the South Atlantic, however, it penetrates the Sub-Antarctic Zone as far as the Antarctic Convergence, and in the Antarctic Zone it may be represented by *V. antarctica.*

Vanadis tagensis Dales, 1955 (characters emended)

(Text-fig. 9)

Type locality. Monterey Bay, California, in a depth of 1,000 to 500 metres.

Vanadis tagensis Dales, 1955, pp. 436–439, figs. *1a, b, c.*

DESCRIPTION. No complete specimens of this species were collected; the longest head fragment is 51 mm. in length for sixty pairs of parapodia. There are six antennae in this species not five as noted in the original description. Text-fig. 9 has been prepared from a paratype in the B.M. (N.H.) collections, Reg. No. 1955.9.30.4 and shows, apart from the anterior dorsal and ventral pairs, and the fifth unpaired on the top of the prostomium, a sixth antenna in the anterior region of the prostomium above and between the ventral pair. This sixth antenna is small and, after preservation in formalin, may be difficult to see. There are twelve terminal papillae on the proboscis of which two lateral pairs are the longest, being about twice as long as the dorsal and ventral groups of four. There are four pairs of tentacular cirri on three successive segments behind the head arranged thus $1 + 1 + 1/1$. The most anterior of these is almost joined ventrally by basal ceratophores. The anterior seven parapodia are much reduced with small cirri and aciculae; they may have a few chaetae present. Thereafter cirri are well developed and ovate, the dorsal twice as long as the ventral and the pedal lobe prominent. In mature females the dorsal cirri of the first two parapodia are modified as receptacula seminis. Chaetae are long and compound. None of the specimens available is sufficiently well preserved to permit a critical diagnosis of the arrangement of the pigmented segmental glands.

DISCUSSION. This species presents two characteristics met nowhere else in the genus, six antennae and four pairs of tentacular cirri, and should be considered quite distinct from known species. It may be that its distinctive habitat (it is the only *Vanadis* known to inhabit deep water exclusively, see below p. 442) provides a key to this disposition of normally stable features.

GENERAL DISTRIBUTION. *V. tagensis* is at present known only from deep water in the North Pacific Ocean, south of the Sub-Arctic Zone (see below, pp. 442, 446–447).

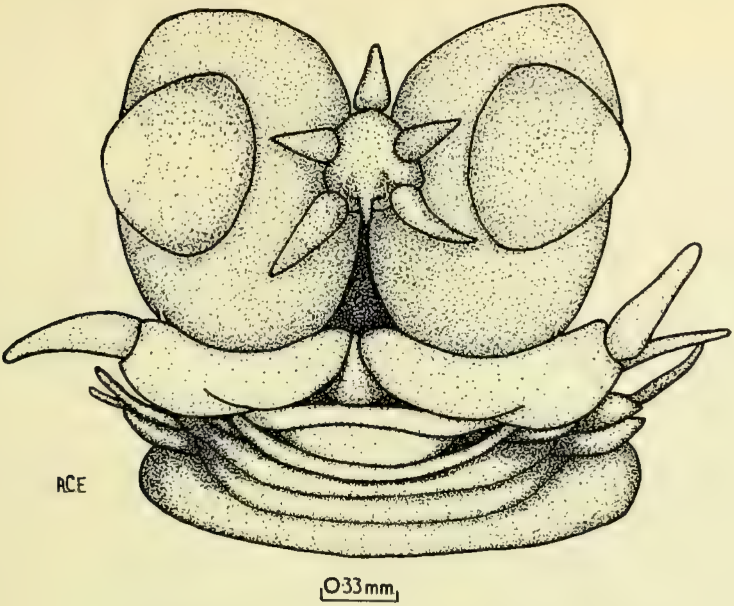

FIG. 9. *Vanadis tagensis*: ventral view of head showing six antennae: Paratype, B.M. (N.H.), Reg. No. 1955.9.30.4.

Genus ***RHYNCHONERELLA*** Costa, 1862

(Emended Claparède, 1868 pro *Rhynchonereella* Costa, 1862)

Body normally elongate. Prostomium extending beyond the eyes and carrying five antennae. Five pairs of tentacular cirri. Parapodia with a cirriform appendage on the pedal lobe; acicular chaetae simple or compound; long slender chaetae (capillaries) always compound.

Type species. *Rhynchonerella gracilis* Costa, 1862.
Type locality. Gulf of Naples.

KEY TO SPECIES

1. With simple acicular chaetae 2
–. With compound acicular chaetae 3
2. Simple acicular chaetae present on the first six to ten chaetigers, but compound capillaries absent (Text-fig. 11); both types of chaetae on remaining feet. Acicular chaetae with a few distal spines (Text-fig. 11) . . . . . ***R. mobii***
–. Simple acicular chaetae and compound capillary chaetae present from the first parapodia (Text-fig. 10*a*). Acicular chaetae smooth . . . . . . ***R. gracilis***
3. Compound acicular chaetae with a large, serrated terminal article (Text-fig. 12*a*–*c*) ***R. petersii***
–. Compound acicular chaetae with a small, sooth terminal article (Text-fig. 14*c*) ***R. angelini***

Rhynchonerella gracilis Costa, 1862

(Text-fig. 10*a*, *b*)

Rhynchonereella gracilis Costa, 1862, p. 168, pl. 4, figs. 13–15.
Callizona nasuta Greeff, 1876, p. 72, pl. VI, figs. 60–62.
Callizona japonica Izuka, 1914, pp. 7–8, pl. 1, fig. 8.
Callizona nasuta: Fauvel, 1923, pp. 215–216, fig. 81*a–c*.
Rhynchonerella gracilis: Støp-Bowitz, 1948, p. 36.
Callizona nasuta: Uschakov, 1957*a*, pp. 279–281, Chart 2, fig. 6*a–d*.

DESCRIPTION. Most specimens collected were anterior pieces rarely measuring more than 8 mm. in length but one complete specimen, from Stn. 112A of the Trans-Pacific Expedition is 20·5 mm. long for 116 chaetigers. The specimen reported by Izuka, (1914 as *C. japonica*) from Misaki measured 36 mm. for about 190 segments. The proboscis is covered with small papillae, all of the same size; there are no terminal papillae. The prostomium protrudes prominently in front of the eyes and carries two pairs of anterior foliaceous antennae with a smaller unpaired antenna between the eyes. Two parallel lines of light brown pigment run down the middle of the protruding prostomium (these may not always be well preserved). The five pairs of tentacular cirri are arranged on three successive segments behind the head thus 1 + 1/1 + 1/1; of these the dorsal are the longest and the posterior the longer. Pigmented segmental glands are present on every chaetiger from the first (these are only rarely not visible). One or two simple acicular chaetae appear on anterior feet with a bundle of long compound capillaries. On posterior feet there is only one acicular chaeta. There is a very prominent cirriform pedal lobe on all feet. The body is terminated by an unpaired anal cirrus.

GENERAL DISTRIBUTION. *R. gracilis* is known only from Tropical and Sub-Tropical waters (see below, pp. 446, 450–451).

Rhynchonerella mobii (Apstein), 1893

(Text-fig. 11)

Type locality. Mediterranean Sea.

Callizona Mobii Apstein, 1893, p. 147.
Callizona Moebii: Fauvel, 1923, pp. 213–214, fig. 80*a–d*.
Rhynchonerella Mobii: Støp-Bowitz, 1948, p. 34.
Rhynchonerella mobii: Dales, 1957, pp. 131–132, figs. 39, 40–43.

DESCRIPTION. The majority of specimens collected are incomplete anterior fragments, less than 15 mm. in length, but from Northern Holiday Expedition Stn. 54 there is an almost complete specimen measuring 45 mm. in length for approximately 170 chaetigers. The prostomium protrudes in front of the eyes and

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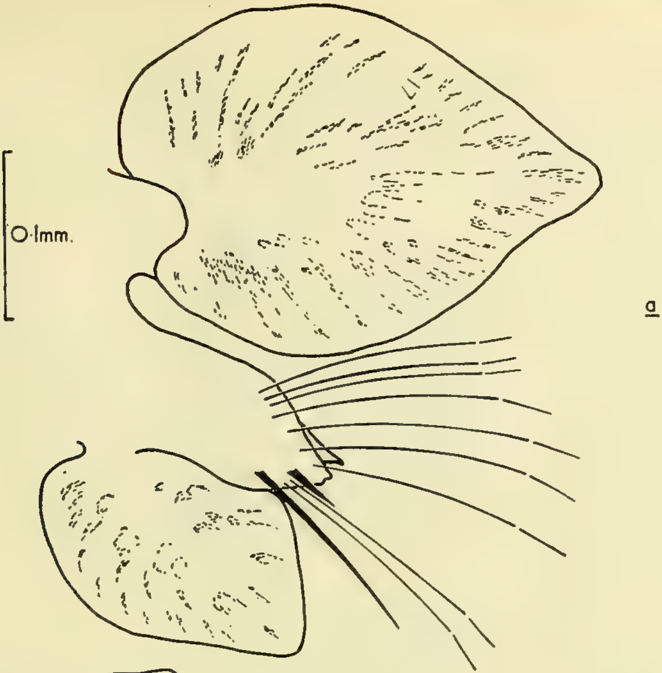
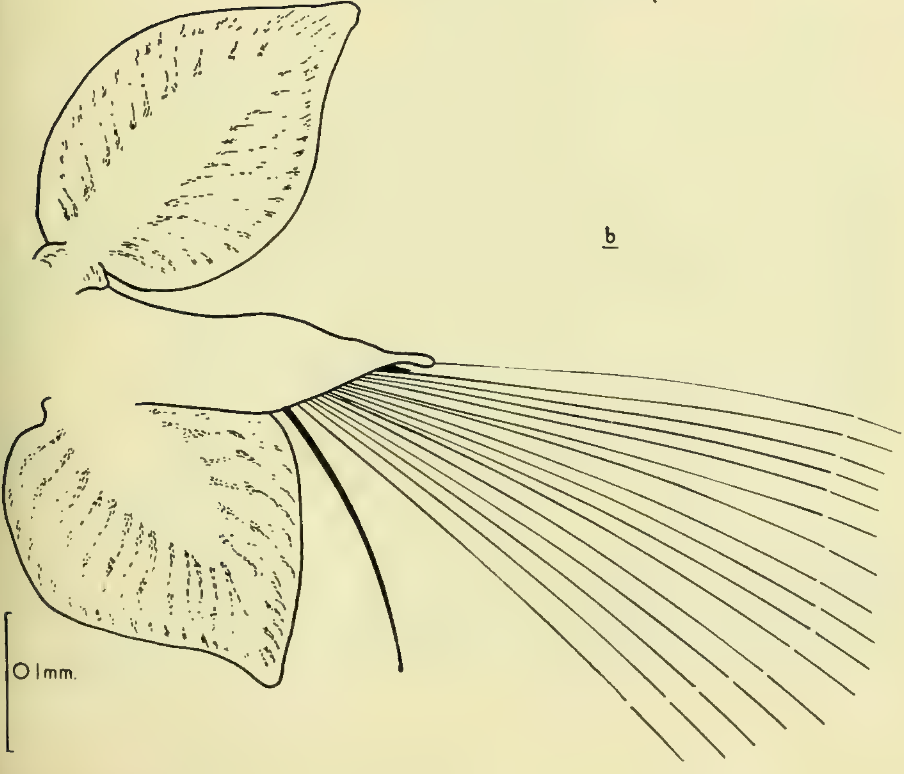
FIG. 10. *Rhynchonerella gracilis:* parapodia, (*a*) from second chaetiger of specimen from Stn. 107A or the Trans-Pacific Exp., (*b*) from ninetieth chaetiger of specimen from Stn. 117A.


0·1mm.
a


b
0·1mm.

carries two pairs of stout anterior antennae and a single small, unpaired, antenna between the large eyes. The five pairs of tentacular cirri are arranged on three successive segments behind the head thus 1 + 1/1 + 1/1 : of these the anterior is short and fat ; the two dorsal are strap-like, equal in length and the longest of all ; the anterior ventral very short and fat ; the posterior ventral broadly foliaceous.

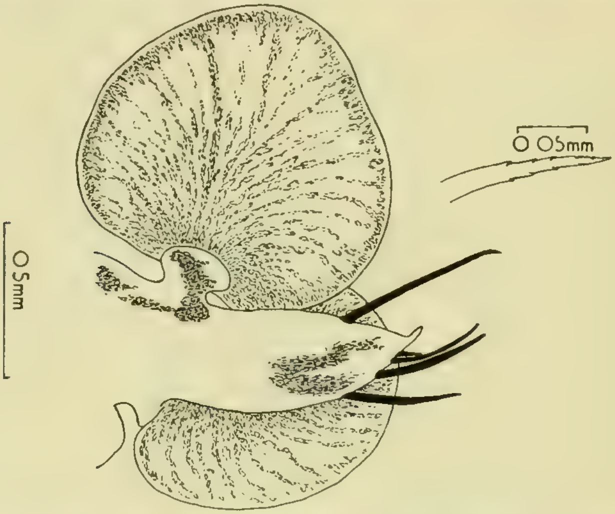


Fig. 11. *Rhynchonerella mobii :* parapodium from the fifth chaetiger of specimen from Stn. 86B of the Trans-Pacific Exp., with acicular chaeta enlarged.

Pigmented segmental glands appear on every foot from the seventh on the few specimens in which they are visible. Anterior parapodia have three to six simple acicular chaetae only ; from the tenth to the twelfth foot compound capillary chaetae appear and acicular chaetae are gradually reduced until there is only one in each foot. The distal ends of the acicular chaetae are slightly serrated ; this serration is visible only at high magnifications. Dorsal and ventral cirri are broadly foliaceous, the former being the larger. There is a very prominent pedal lobe on all parapodia.

General distribution. *R. mobii* is known only from Tropical and Sub-Tropical waters (see below, pp. 446–449).

Rhynchonerella petersii (Langerhans), 1880*

(Text-fig. 12*a*, *b*, *c*)

Type locality. Madeira.

Alciopa (*Halodora*) *Petersii* Langerhans, 1880, p. 312, pl. XVII, fig. 49.
Callizona setosa : Fauvel, 1923, p. 214, fig. 80*c*, *f*.
Rhynchonerella petersii : Støp-Bowitz, 1948, p. 34.
Callizona setosa : Uschakov, 1957*a*, p. 281, chart 2, fig. 6*e*–*i*.

* See Addenda, p. 492.

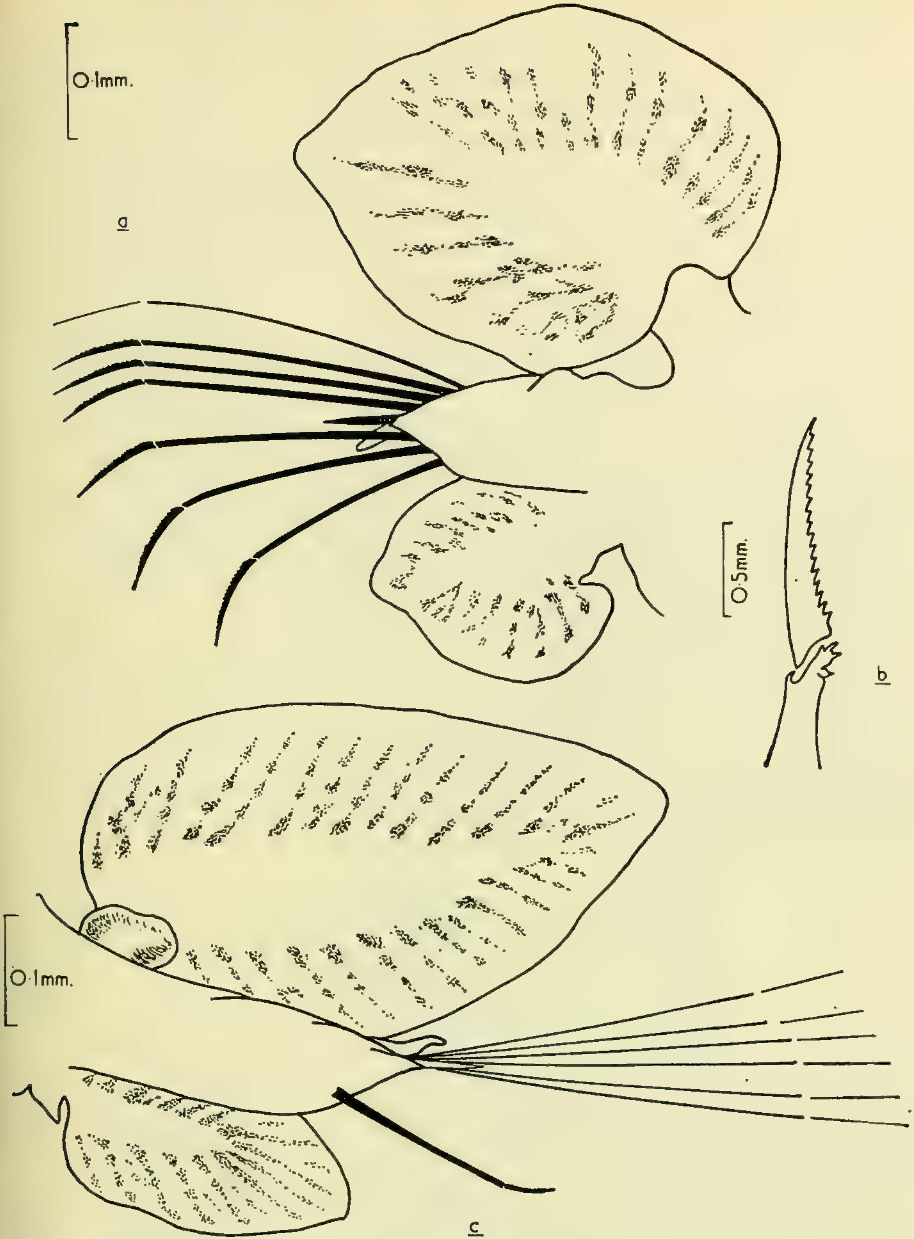


FIG. 12. *Rhynchonerella petersii* : (*a*) parapodium, from the fourth chaetiger of specimen from Stn. 11A of the Trans-Pacific Exp., (*b*) compound acicular chaeta from anterior chaetiger of specimen from Stn. 129B, (*c*) parapodium from the fourteenth chaetiger of specimen from Stn. 12E.

DESCRIPTION. Only fragments of this species were collected, the largest measuring 10 mm. in length for forty-two chaetigers. The prostomium projects only a little way in front of the eyes and carries four bulbous terminal antennae and one very small median antenna between the eyes. The prostomium, antennae and interior edge of the eyes may be sprinkled with light brown spots. The five pairs of tentacular cirri are arranged on three successive segments between the head thus 1 + 1/1 + 1/1; the anterior one is long and strap-like; the two dorsals are the longest and the posterior one the longer, both pointed; the anterior ventral is very short and digitiform; the posterior ventral small and foliaceous. The proboscis carries twelve small terminal papillae. On anterior parapodia dorsal cirri are large and broadly foliaceous, ventral cirri smaller but of similar shape. On the first four to six parapodia acicular chaetae are much more numerous than compound capillary chaetae; on a specimen from Trans-Pacific Expedition Stn. 3A, for example, there are twelve compound acicular chaetae and one compound capillary chaeta on the first parapodia—see also Text-fig. 12*a* for a specimen from Stn. 11A, which has these chaetae in the proportion of 6 : 1 respectively. From the fourth to sixth feet posteriorly there is a reduction in the number of compound acicular chaetae and an increase in the compound capillaries. The terminal article of all the compound acicular chaetae is denticulated and at high magnification the distal end of the main stem is seen to bear spines. All parapodia carry a prominent cirriform pedal appendage. Pigmented segmental glands may appear on every chaetiger from the third but they are frequently not distinctly preserved.

DISCUSSION. This is the first time that spines have been reported on the distal end of the main stem of acicular chaetae in *R. petersii*. I have checked a specimen of the same species deposited in the B.M. (N.H.) Fauvel Collection (Reg. No. 1928.4.26.746 from the Balearic Islands, Fauvel, 1916 as *Callizona setosa*) and find it identical with the above in this and all other respects.

GENERAL DISTRIBUTION. *R. petersii* is known only from Tropical and Sub-Tropical waters (see below, pp. 446, 448).

Rhynchonerella angelini (Kinberg), 1866

(Text-figs. 13, 14, *a*, *b*, *c*)

Type locality. China Sea, 20° S., 107° E.

Krohnia Angelini Kinberg, 1866, p. 242.
Callizona Angeliin: Fauvel, 1923, p. 215, fig. 81*d–i*.
Callizona angelini: Berkeley & Berkeley, 1948, pp. 40–41, fig. 56.
Rhynchonerella Angelini: Støp-Bowitz, 1948, pp. 34–36.
Rhynchonerella angelini: Dales, 1957, p. 113, figs. 44–46.
Rhynchonerella angelini: Tebble, 1960, p. 192; p. 255, fig. 50.

DESCRIPTION. This is the only species of *Rhynchonerella* which is normally complete when collected; it is comparatively large and robust, the longest specimens

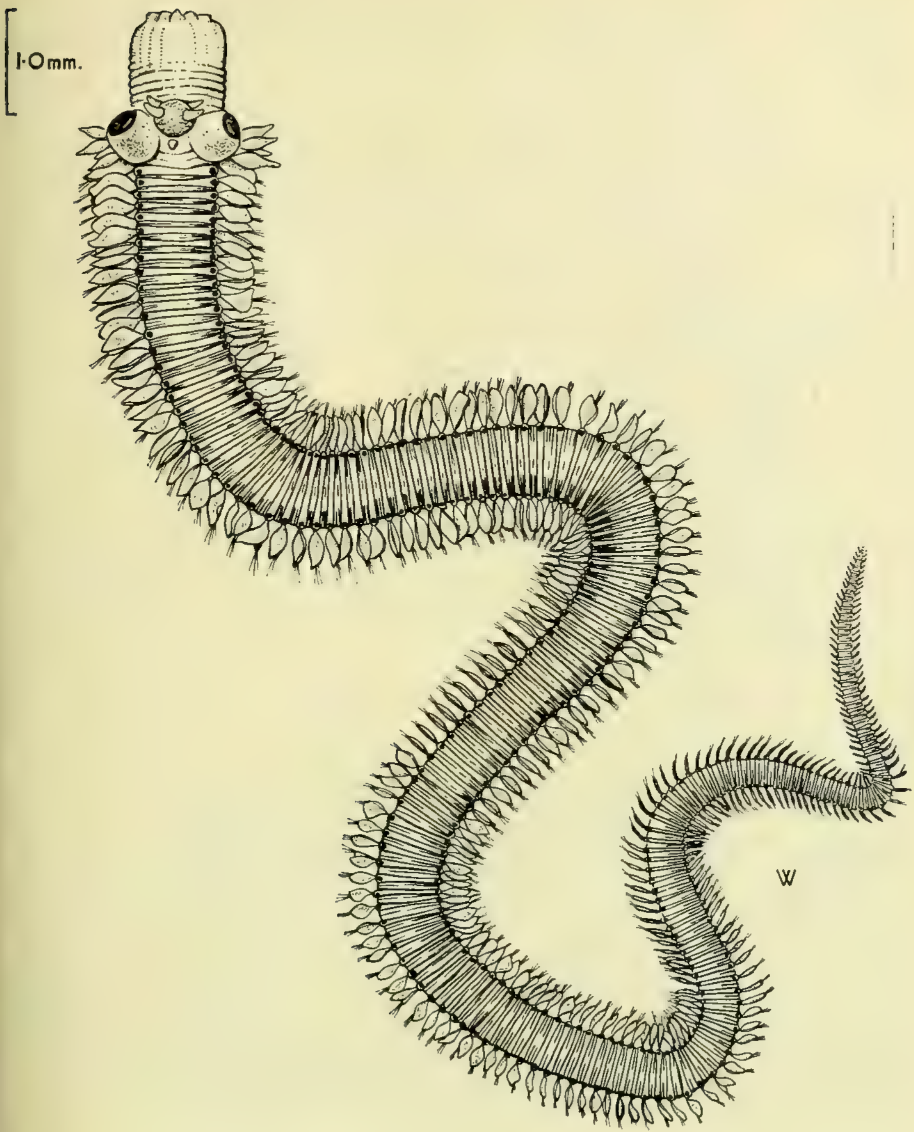


FIG. 13. *Rhynchonerella angelini :* specimen from Stn. 117B of the Trans-Pacific Exp.

measuring 70 mm. in length and the smallest 10 mm. The prostomium protrudes in front of the eyes and carries two pairs of anterior short, dumpy antennae, and a small unpaired antenna immediately behind this prostomial extension, between the large eyes. The prostomium, tentacular cirri, antennae and anterior parapodia are normally covered with a brown pigment. The proboscis is covered with papillae between which there are longitudinal grooves on the anterior half and lateral grooves on the posterior half. The five pairs of tentacular cirri are arranged on three suc-

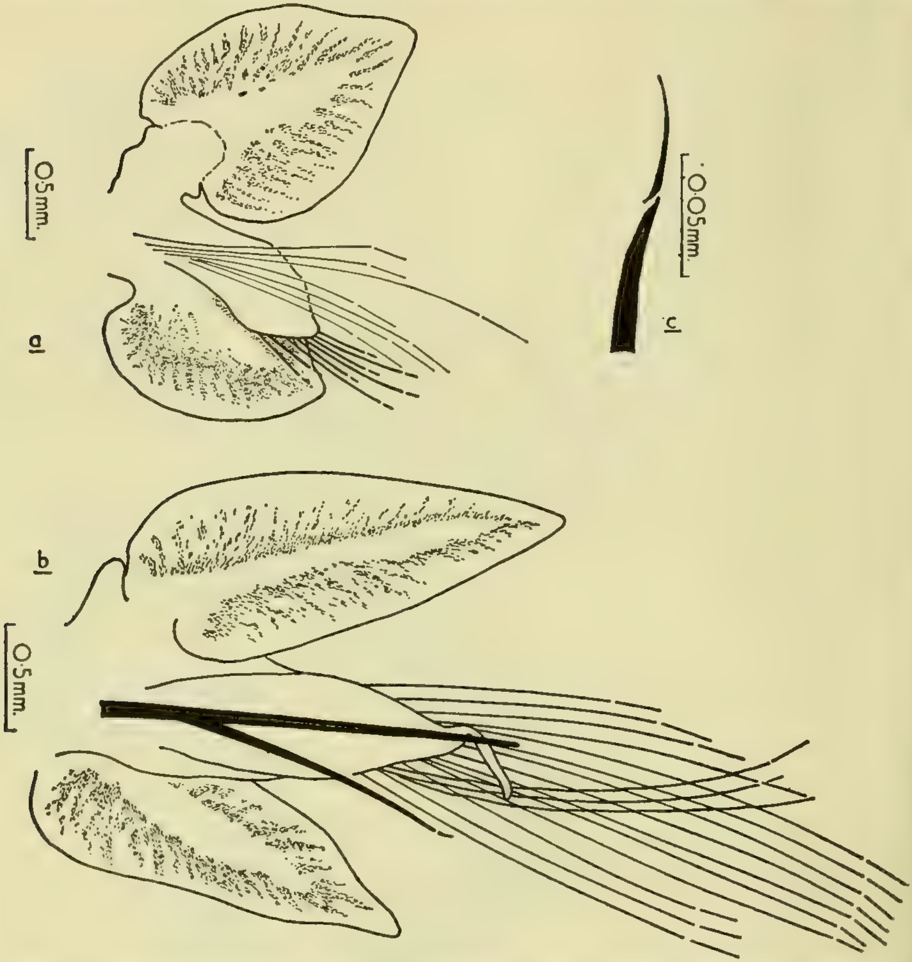


FIG. 14. *Rhynchonerella angelini :* (*a*) parapodium from the fourth chaetiger of specimen from Stn. 50B of the Trans-Pacific Exp., (*b*) the same from the eighteenth chaetiger, (*c*) compound acicular chaeta of specimen from Stn. 117B.

cessive segments between the head thus 1 + 1/1 + 1/1 of these the anterior is short and pointed and the two dorsal long and pointed, the two ventral are short and tend to be foliaceous; all are thick at the base. Over the anterior three-quarters of the body parapodia have broadly foliaceous dorsal cirri which become elongate posteriorly and smaller but still large foliaceous ventral cirri. The first six to ten parapodia have two types of chaetae, an inferior group of stout acicular bristles with short terminal articles and a superior group of compound capillary chaetae with long terminal articles. The acicular chaetae decrease rapidly in number after these first parapodia and are absent over the greater part of the body. On all parapodia there is a prominent cirriform pedal appendage. Posteriorly the body width is considerably reduced assuming the appearance of a whip-cord-like tail.

General distribution. *R. angelini* is confined to Tropical and Sub-Tropical waters in the southern hemisphere but in the northern extends into higher latitudes (see below, pp. 450, 452).

Genus ***PLOTOHELMIS*** Chamberlin, 1919

Body elongate. Prostomium extending beyond the eyes and carrying five antennae. Five pairs of tentacular cirri. Parapodia without a cirriform appendage on the pedal lobe; acicular chaetae simple, capillary chaetae compound.

Type species. *Plotohelmis alata* Chamberlin, 1919.

Type locality. South Pacific Ocean.

Plotohelmis tenuis (Apstein), 1900

(Text-figs. 15*a*, *b*; 16, 17)

Original localities. Tropical Atlantic Ocean.

Corynocephalus tenuis Apstein, 1900, p. 14, pl. 2, figs. 14–16.
Corynocephalus tenuis: Chamberlin, 1919, p. 141.
Plotohelmis tenuis: Dales, 1957, pp. 125–128, figs. 36–39.

Description. No complete specimens of this species were collected; the longest fragment measures 25 mm. in length. The prostomium projects forward between the eyes as a bulbous outgrowth divided into hemispheres by a median groove; there are four terminal antennae on this outgrowth, two dorsal and two ventral, all are small; the dorsal pair are fat and the ventral thin. There is a pit at the anterior end of the prostomium in which the antennae have their bases. (This pit, which may be filled with extraneous material, should not be confused with the opening of the proboscis which may, or may not, be extruded.) A fifth unpaired antenna is situated on top of the prostomium between the large eyes. When fully extruded the proboscis carries numerous small papillae terminally. There are five pairs of tentacular cirri arranged on successive segments behind the head thus 1 + 1/1 + 1/1.

Of these the posterior ventrals are very small and foliaceous, the posterior dorsals very long and thin, and the anterior lanceolate, of medium length. Parapodia have no cirriform appendage on the pedal lobe, dorsal cirri are large, broadly foliaceous, and ventral cirri cirriform, smaller than the pedal lobe; chaetae are simple aciculars and compound capillaries with long thin terminal articles. Pigmented segmental glands, when preserved, appear at about the ninth foot, becoming larger posteriorly so that they extend along the body wall as a lateral band. Anterior parapodia may have up to a dozen stout acicular chaetae, and no compound

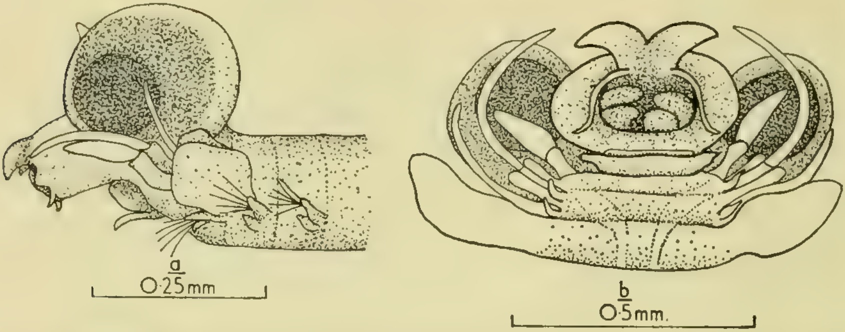


FIG. 15. *Plotohelmis tenuis*: (*a*) lateral view of head and anterior segments of specimen from Stn. 1A of the Trans-Pacific Exp., (*b*) the same, ventral view.

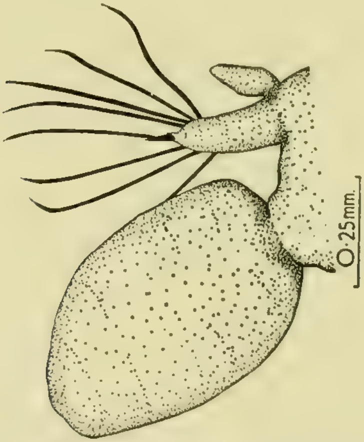


FIG. 16. *Plotohelmis tenuis*: parapodium of the fourth chaetiger of specimen from Stn. 1A of the Trans-Pacific Exp.

capillaries, but from about the sixth foot the latter begin to replace the former till there may be only one acicular chaetae present, always in the most ventral position.

DISCUSSION. Dales (1957) was the first to establish that this species is *Plotohelmis* but I have found no specimens which support his separating the three species within the genus *P. tenuis*, *P. alata* and *P. capitata*, on relative lengths of tentacular cirri.

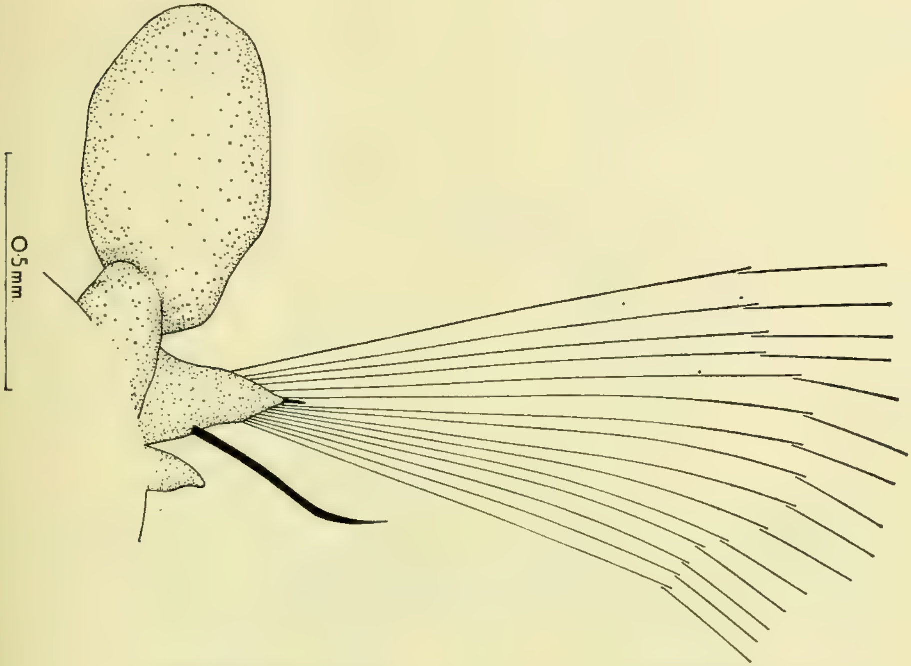


FIG. 17. *Plotohelmis tenuis* : parapodium of the thirtieth chaetiger of specimen from Stn. 1A of the Trans-Pacific Exp.

GENERAL DISTRIBUTION. *P. tenuis* occurs mainly in Tropical and Sub-Tropical waters but may occasionally be found in higher latitudes (see below, pp. 450, 453–4).

Genus ***KROHNIA*** Quatrefages, 1865

Body elongate. Five pairs of tentacular cirri. Parapodia with a cirriform appendage on the pedal lobe, with simple capillary and acicular chaetae only.

Type species. *Alciopa lepidota* Krohn, 1845.

Type locality. Messina, Mediterranean Sea.

Krohnia lepidota (Krohn), 1845

(Text-fig. 18)

Alciopa lepidota Krohn, 1845, p. 175.
Krohnia lepidota: Quatrefages, 1865, pp. 158–159.
Rhynchonerella cincinnata Chamberlin, 1919, pp. 146–147.
Callizona lepidota: Fauvel, 1923, pp. 211–212, fig. 79*e–h*.
Krohnia lepidota: Støp-Bowitz, 1948, p. 33.
Callizonella lepidota: Uschakov, 1957*a*, p. 278, Chart 2, fig. 5.
Krohnia lepidota: Dales, 1957, p. 129.
Krohnia lepidota: Tebble, 1960, p. 193; p. 255, fig. 50.

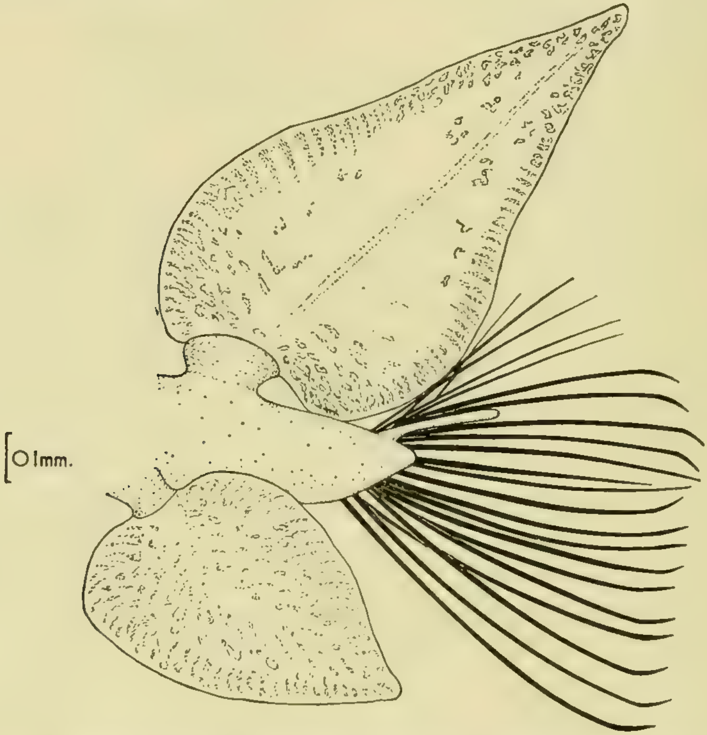


FIG. 18. *Krohnia lepidota:* parapodium of the second chaetiger of specimen from Stn. 120A of the Trans-Pacific Exp.

DESCRIPTION. No complete specimens of this species were collected. The largest fragments rarely measure more than 15 mm. long; Fauvel (1923) gives a maximum of 100 mm. for the length of a complete specimen. Two pairs of small but stout conical antennae are situated on the anterior border of the prostomium and an unpaired antenna occurs dorsally between the eyes. The proboscis is smooth, except for a broad group of small terminal papillae. The five pairs of tentacular cirri appear on successive segments behind the head thus 1 + 1/1 + 1/1; of these the anterior is long, strap-like and pointed; the two ventrals foliaceous and a little smaller; the anterior dorsal long and thin and the posterior dorsal exceedingly long, reaching out as far again as the total body width. Few of the parapodial cirri have been retained but on one anterior foot the dorsal cirrus is very large and foliaceous and the ventral smaller, and broadly foliaceous. Chaetae are of two types, simple stout acicular chaetae and simple capillaries, the former are more numerous anteriorly and are gradually replaced by the latter posteriorly. The whole body surface is sprinkled with black spots, which run in lines along the antennae and tentacular cirri and are scattered over the eyes and prostomium; they are arranged in a linear series at the dorsal edge of the parapodia and ventrally at the base of the feet and in pairs on the mid-ventral line; the anterior surface of each pedal lobe has a single black spot in its centre. These spots show clearly only in well preserved specimens, but in all material they are present and even when some have disappeared, an overall pattern similar to that described can be visualized.

DISCUSSION. Chamberlin's (1919) records of *Rhynchonerella cincinnata* Greeff, 1876, from the Pacific must be considered as *K. lepidota* for although he does not describe the pigment spots he refers to the very long posterior tentacular cirri, which appear to be characteristic. Dales (1957) reports *Callizona pigmenta* Treadwell, 1943, as synonymous with *K. lepidota.*

GENERAL DISTRIBUTION. *K. lepidota* is known only from Tropical and Sub-Tropical waters (see below pp. 454–455).

Family TYPHLOSCOLECIDAE

Exclusively pelagic. Body spindle-shaped or cylindrical. Prostomium not distinctly marked off from the rest of the body. Nuchal organs well developed. Peristomium indistinct bearing one pair of cirri; the two succeeding segments also bear only one pair but thereafter there are two representing the dorsal and ventral cirri of the parapodia. Pedal mamelon reduced with an acicula and a few small simple chaetae sometimes present.

KEY TO GENERA

1. Prostomium with dorsal and ventral ciliated epaulettes . . . . ***TYPHLOSCOLEX***
–. Prostomium without ciliated epaulettes 2
2. With a pair of nuchal organs which are attached to the body only along their anterior border; a caruncle may or may not be present . . . ***TRAVISIOPSIS***
–. With nuchal organs entirely attached to the body surface . . . ***SAGITELLA***

Genus ***TYPHLOSCOLEX*** Busch, 1851

Body spindle-shaped. Prostomium with dorsal and ventral ciliated epaulettes, the dorsal epaulettes carrying two lateral basal wings. Chaetae begin on the fifth parapodia. Protrusible proboscis.

Type species. *Typhloscolex mülleri* Busch, 1851.*

Type locality. Trieste.

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* See Addenda, p. 492.

Typhloscolex mülleri Busch, 1851

Typhloscolex mülleri Busch, 1851, pp. 115–116, pl. 11, figs. 1–6.
Typhloscolex Mülleri : Fauvel, 1923, pp. 226–227, fig. 85, *f–h*.
Typhloscolex Mülleri : Støp-Bowitz, 1948, pp. 17–18, fig. 8.
Typhloscolex mülleri : Uschakov, 1955, p. 112, figs. *a–c*.
Typhloscolex mülleri : Uschakov, 1957*a*, p. 286, Chart 4.
Typhloscolex mülleri : Dales, 1957, pp. 146–147, fig. 55, *a–b*.
Typhloscolex mülleri : Tebble, 1960, pp. 195–196 and pp. 231–236, figs. 34–36, Tables 16, 17.

DESCRIPTION. In Table IV the size range of specimens of *T. mülleri* collected on the Trans-Pacific Expedition at Stations 12A to 21B have been listed. This

TABLE IV.—*Typhloscolex mülleri**

Number of specimens between
1·5 mm. and 14·0 mm.
in length

Stn.														
21B	1	2	3	3	2	4	2	1	7	3	1	1	—	Sub-Arctic Zone
21A	—	—	—	2	2	—	2	1	1	4	1	—	—	
20B	—	—	—	2	—	—	4	3	3	3	1	2	2	
20A	1	—	4	7	3	11	6	1	2	1	—	1	—	
19B	—	—	—	—	—	2	2	1	1	4	3	2	1	
19A	—	—	4	2	3	2	—	—	1	—	—	—	—	
18B	—	1	1	—										Transition Zone
18A	—	—	1	—										
17A	—	—	2	2										
16E	—	—	—	1										
16B	—	—	—	1										
16A	1	—	1	1										
15B	—	1	—	—										
15A	—	1	—	—										
14B	—	2	—	—										Sub-Tropical Zone
14A	—	1	—	—										
13B	1	2	—	—										
13A	—	2	1	1										
12F	—	1	1	1										
12D	—	1	1	1										
12C	—	2	3	—										
12B	—	1	—	—										
12A	—	1	—	—										

* This Table also shows the increase in numbers of *T. mülleri* caught in the Sub-Arctic Zone and that an ecotypic form of this species inhabits this zone ; these points are examined in greater detail later.

line of stations crosses from the Sub-Tropical Zone through the Transition Zone into the Sub-Arctic Zone.

A finely pointed prostomial palpode projects between the dorsal and ventral ciliated epaulettes; the latter are always as wide as the body width. The dorsal epaulette carries two basal wings which are proportionally larger in the bigger specimens. On each side of the peristomium are the first cirri, large and kidney-shaped, covering the epaulettes laterally. The next two segments carry one oval cirrus on each side; thereafter foliaceous dorsal and ventral cirri are present on all segments up to the end of the body. Simple chaetae appear on the fifth parapodia. There is a pair of elliptical anal cirri.

DISCUSSION. A most striking feature of the systematic analysis of these collections was the occurrence of specimens of *T. mülleri*, measuring up to 13–21 mm. in length, at stations made in the Sub-Arctic Zone. Samples from this zone were recognizable immediately through their presence; they have been reported from nowhere else in the world. Almost all previous authorities accepted 2–7 mm. as the approximate size range of *T. mülleri*, only Uschakov (1955 and 1957*a*) having previously reported a larger size, 2–15 mm., and these from the Bering Sea, the Sea of Okhotsk and off the south-east coast of Kamchatka, within the Sub-Arctic Zone of the North Pacific.

Statistical analysis[1] of the data in Table IV indicated that the animals from the Sub-Arctic Zone on the one hand and the Transition and Sub-Tropical Zones on the other did not belong to the same population ($F = 21{\cdot}2$; d.f. 2,156; $P < 0{\cdot}001$) and that the Sub-Arctic Zone general mean (7·51 mm.) was significantly greater than the Transition Zone (4·57 mm.) which was non-significantly greater than the Sub-Tropical Zone (4·04 mm.). This final analysis also indicated that the Transitional and Sub-Tropical Zone data were homogenous whilst the sub-arctic data could be resolved into two populations the one with smaller individuals (4·2 mm.) being closely similar to that from the other zones, whilst the other had significantly greater (9·1 mm.) individuals.

As isolated specimens the larger forms in the Sub-Arctic Zone could have been described as separate species, relating specific characteristics only to gross size, but the presence of typical small forms is against this. The evidence from statistical analysis, however, suggests that there are two distinct populations, a population of small individuals, which is part of a population occurring in all three zones, and a population of large forms which is confined to the Sub-Arctic Zone. Presumably we have here an ecotypic variation (large forms adapted to the sub-arctic environment) mixed with members of a more widely distributed continuous series of contiguous populations.

GENERAL DISTRIBUTION. *T. mülleri* is a cosmopolitan species, having been reported from all explored water masses (see below, pp. 454, 456).

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[1] These analyses were carried out by Mr. D. E. Davies and involved in order, an analysis of variance, a sequential means test based on the error of variance derived from the first analysis, and tabulated upper 5% range tests followed by a polymodal graphical analysis due to Harding (1949). Statistical treatment of these data was first suggested by Dr. E. W. Fager of the Scripps Institution of Oceanography.

Genus ***SAGITELLA*** Wagner, 1872

Body spindle-shaped. Prostomium with nuchal organs which are entirely fixed to the body surface. Caruncle absent. Simple chaetae appearing from about the third to fifth parapodia.

Type species. *Sagitella kowalewskii* forme A. Wagner, 1872.

Type locality. Tropical Atlantic Ocean.

The second *w* in *kowalewskii* has frequently been altered to a *v*; there is no valid reason for altering the original orthography in this case and I therefore use the spelling *kowalewskii*.

Sagitella kowalewskii Wagner, 1872

Sagitella **kowalewskii** forme A Wagner, 1872, pp. 342–347, figs. A–C.
Sagitella kowalewskii: Fauvel, 1923, p. 228, fig. 85, *a–c*.
Sagitella kowalevskii: Støp-Bowitz, 1948, pp. 56–57, fig. 43.
Plotobia paucichaeta: Treadwell, 1943, p. 38, pl. 11, fig. 26.
Sagitella kowalewskii: Uschakov, 1957*a*, pp. 288–289, Chart 4.
Sagitella kowalevskii: Dales, 1957, pp. 147–148, figs. 56, 57, 60

DESCRIPTION. The largest specimen collected measures 19 mm. in length for about sixty pairs of parapodia and the smallest 2·0 mm. for thirty. The prostomium has a finely pointed palpode projecting anteriorly. The first three segments carry one foliaceous cirrus on each side. Between the first and second of these, on the dorsal surface, the nuchal organs form two boomerang-shaped ridges. Parapodia carry a pair of dorsal and ventral cirri, with simple chaetae first appearing on the third to fifth feet; these are clearly visible only on posterior segments where the segmentation is more clearly marked. The pygidium carries two spatulate anal cirri.

DISCUSSION. I have examined a syntype of *Plotobia paucichaeta* Treadwell 1943, in the collections of the U.S.N.M., No. 130492, from 14° 52′ S., 126° 07′ W., and find it is a *Sagitella kowalewskii*: this confirms the opinion of Dales (1957). From Treadwell's description of *Plotobia paucichaeta* I thought it might be *Travisiopsis dubia* (q.v.).

GENERAL DISTRIBUTION. *S. kowalewskii* is known only from Tropical and Sub-Tropical waters (see below, pp. 454, 457–8).

Genus ***TRAVISIOPSIS*** Levinsen, 1885 (characters emended)

Body cylindrical or spindle-shaped. Prostomium with nuchal lobes which are free from the body over the greater part of their length; these normally flank a caruncle but in one species (*T. dubia*) a true caruncle is absent. The first three segments behind the head with single foliaceous cirrus on each side; thereafter parapodia with paired foliaceous cirri; only a few simple chaetae present on some parapodia.

Type species. *Travisiopsis lobifera* Levinsen, 1885.

Type locality. 42° 50′ N., 46° 10′ W.

This description of *Travisiopsis* is emended to include *Travisiopsis dubia* Støp-Bowitz, 1948, which was first described from two specimens collected by the *Michael Sars* in the North Atlantic. Sixteen more are reported here, and it is clear that this species though without a true caruncle (but only a thickening of the dorsal surface of the prostomium) is a *Travisiopsis* because it has two nuchal lobes which are free from the body over the greater part of their length. It differs, therefore, fundamentally from the closely related *Sagitella*, which has neither caruncle, nor free nuchal lobes, but has these latter organs entirely attached, forming distinct ridges.

KEY TO SPECIES

1. Caruncle absent	***T. dubia***
–. Caruncle present	2
2. Nuchal lobes branches	***T. coniceps***
–. Nuchal lobes not branched	3
3. Nuchal lobes long, finger-shaped	***T. lanceolata***
–. Nuchal lobes short	4
4. Caruncle round ; twenty-one segments	***T. lobifera***
–. Caruncle rectangular, twenty-five segments	***T. levinseni***

Travisiopsis lobifera Levinsen, 1885

(Text-fig. 19)

Travisiopsis lobifera Levinsen, 1885, pp. 336–340, figs. 17–20.
Travisiopsis lobifera : Fauvel, 1923, p. 229, fig. 86*a–d*.
Travisiopsis lobifera : Støp-Bowitz, 1948, pp. 57–58, fig. 44.
Travisiopsis lobifera : Uschakov, 1957*a*, pp. 286–287, Chart 4, fig. 7, *d–g*.
Travisiopsis lobifera : Berkeley & Berkeley, 1957, pp. 577–578.
Travisiopsis lobifera : Dales, 1957, pp. 148–149, figs. 58–60 (in part).
Travisiopsis lobifera : Tebble, 1960, pp. 196–197, fig. 13*a* ; p. 245, fig. 45.

DESCRIPTION. This species is cylindrical in shape and may measure up to 25 mm. long for a constant twenty-one segments. The median dorsal caruncle, attached on a level with the first cirri, is characteristically oval. Paired nuchal lobes surround the caruncle in the form of fixed processes anteriorly, and laterally, with free projecting lobes posteriorly which reach as far as the second cirri. The single cirri of the first three segments are circular—except for the incision at the point of attachment—thereafter the parapodial cirri are approximately heart-shaped. Simple acicular chaetae may appear from the fifth segment ; there are rarely more than three of these in a group and there may be only one. Anal cirri are elongate oval to rectangular in form.

DISCUSSION. Dales (1957) refers *Plotobia simplex* Chamberlin (1919) to *T. lobifera* but I agree with Støp-Bowitz (1948) that it is probably *T. lanceolata* (see below, p. 413).

GENERAL DISTRIBUTION. *T. lobifera* is known only from Tropical and Sub-Tropical waters (see below, pp. 458–459).

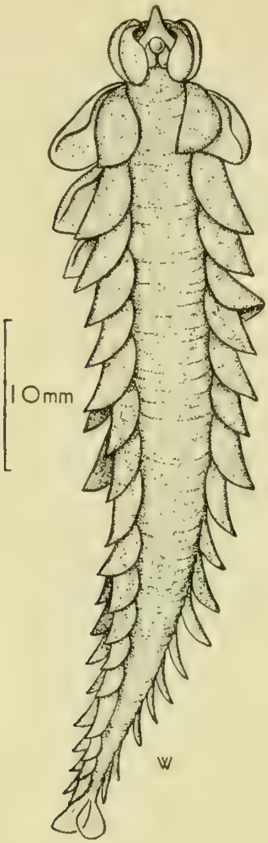

FIG. 19. *Travisiopsis lobifera* : specimen from Stn. 13B of the Trans-Pacific Expedition.

Travisiopsis levinseni Southern, 1910

Type locality. 53° 07′ N., 15° 09′ W., 650–750 fathoms (= 1,188·7–1,371·6 m.).

Travisiopsis levinseni Southern, 1910, p. 429.
Travisiopsis levinseni : Southern, 1911, pp. 32–33, pl. 2, figs. 7–10.
Travisiopsis levinseni : Fauvel, 1923, pp. 229–230.
Travisiopsis levinseni : Støp-Bowitz, 1948, pp. 59–60, fig. 46, fig. 47*a–b*.
Travisiopsis levinseni : Uschakov, 1955, p. 114, fig. 14*d–g*.
Travisiopsis levinseni : Uschakov, 1957*a*, p. 288, Chart 4.
Travisiopsis levinseni : Dales, 1957, p. 150.
Travisiopsis levinseni : Tebble, 1960, pp. 197–198, fig. 13*b* ; pp. 236–237, fig. 36.

Description. This species is spindle-shaped and may measure up to 35 mm. in length for a constant twenty-five segments. The median dorsal caruncle is attached on a level with the first cirri and is characteristically rectangular. Paired nuchal lobes border the caruncle laterally with free projecting semicircular lobes posteriorly, which reach as far as the second cirri. The single cirri of the first three segments are foliaceous; thereafter the paired parapodial cirri are rectangular, becoming lanceolate posteriorly. Simple acicular chaetae may appear from the sixth foot, with rarely more than three in a group. Anal cirri are long and oval.

General distribution. The records of this species from the North Pacific Ocean are too few to warrant drawing any firm conclusions about its distribution (see below, pp. 458, 461). In the South Atlantic Ocean *T. levinseni* has been reported in all hydrological zones (Tebble, 1960); its distribution in the North Atlantic Ocean has not been fully investigated.

Travisiopsis lanceolata Southern, 1910

Type locality. 51° 12′ N., 11° 55′ W., 500 fathoms (914·4 m.).

Travisiopsis lanceolata Southern, 1910, p. 429.
Travisiopsis lanceolata: Southern, 1911, pp. 30–32, pl. 1, figs. 3, 5, 6.
Plotobia simplex Chamberlin, 1919, pp. 155–156, pl. 65, figs. 6–11; pl. 66, fig. 1.
Travisiopsis lanceolata: Fauvel, 1923, p. 229, fig. 86, *e–g*.
Plotobia simplex: Treadwell, 1943, p. 38.
Travisiopsis lanceolata: Støp-Bowitz, 1948, pp. 58–59, figs. 45–46.
Travisiopsis lobifera: Dales, 1957, pp. 148–150, figs. 58–60 (in part).
Travisiopsis lanceolata: Tebble, 1960, pp. 198–199, fig. 13*c*; p. 246, fig. 45.

Description. This spindle-shaped species may measure up to 38 mm. in length for a constant twenty-two segments. The median dorsal caruncle is ∇ in shape; the anterior part is attached at the level of the first cirri, the posterior portion is free. Two long, finger-shaped, nuchal lobes surround the caruncle anteriorly, are free posteriorly and may reach to the fourth segment. Cirri on the first three segments are reniform, thereafter they are almost square becoming lanceolate posteriorly.

Discussion. There can be little doubt that *Plotobia simplex* Chamberlin (1919) is synonymous with *T. lanceolata* as suggested by Støp-Bowitz (1948). Dales (1957) considers *P. simplex* synonymous with *T. lobifera* but Chamberlin's drawing (1919, pl. 66, fig. 1) shows the characteristic finger-shaped nuchal processes clearly.

General distribution. Chamberlin's (1919) record of *P. simplex* appears to be the first for *T. lanceolata* from the North Pacific where it is known from few records (see below, pp. 458, 461). In the South Atlantic Ocean *T. lanceolata* does not occur south of the Sub-Tropical Convergence but in the North Atlantic it has been reported from boreal waters, Wesenberg-Lund (1950, 1951).

Travisiopsis dubia Støp-Bowitz, 1948

(Text-fig. 20, *a*, *b*, *c*)

Type locality. North Atlantic Ocean, 39° 30′ N., 49° 42′ W.

Travisiopsis dubia Støp-Bowitz, 1948, pp. 60–61, fig. 48, *a–e*.
Travisiopsis dubia: Dales, 1960, p. 485.

Description. The holotype of this species measures 6 mm. in length for twenty-eight segments and the paratype 10 mm. for twenty-three segments (Støp-Bowitz, 1948, both specimens in the Bergen Museum, Norway).

Of the sixteen specimens reported here the smallest measures 2·5 mm. in length for eighteen segments and the longest 6·5 mm. for twenty-six.

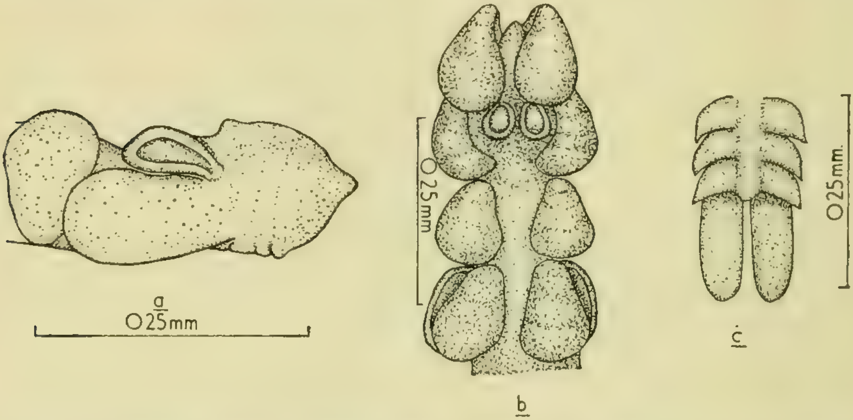

Fig. 20. *Travisiopsis dubia:* specimen from Stn. 92A of the Trans-Pacific Exp., (*a*) side view of head and anterior segments with the anterior pair of cirri omitted, (*b*) dorsal view of head and anterior segments, (*c*) dorsal view of posterior segments.

The slender body terminates anteriorly in a bulbous point. The dorsal nuchal lobes are attached along their anterior edge only, on a level with the anterior border of the second cirri; they are oval to semicircular with a rim along the outer edge. They do not border a caruncle but the dorsal surface of the prostomium in front of them is considerably thicker than elsewhere. The cirri on the first segments are circular and cover the front of the prostomium laterally, on the second segment they are elongate, broadly oval, with the long axis horizontal, and on the third segment also elongate, broadly oval but with the long axis vertical. The first group of paired parapodial cirri are lanceolate but from the middle body region become gradually quadrate up to the end of the body. Simple acicular chaetae appear between some parapodial cirri; there are never more than three of these in a group and they may not penetrate the body wall in posterior segments. Anal cirri are elongate, and curved at their free ends.

Discussion. This is the first record of this species since its original discovery.[1] Dr. C. Støp-Bowitz kindly compared specimens I sent him with the type material and was able to confirm that they are *T. dubia*. There is no doubt that this species is superficially much closer to *Sagitella* than to *Travisiopsis* but it must be included in the latter species because of the free nuchal lobes. Støp-Bowitz (1948) notes this similarity but refers the species to *Travisiopsis* because of the possession of a caruncle. However, it is noted above that *T. dubia* does not have a true caruncle, merely a thickening of the dorsal surface of the prostomium and this character brings it closer still to *Sagitella*. Nevertheless, the possession of nuchal lobes, attached only along their anterior borders, but free posteriorly and not completely attached to form ridges as in *Sagitella*, is a distinctive generic difference and unequivocally establishes the species as a *Traviopsis*.

General distribution. *T. dubia* is known from very few records all of which are from Tropical and Sub-Tropical waters (see below, pp. 460, 461).

Family Phyllodocidae

Not exclusively pelagic. Body normally long and slender with numerous segments except in the pelagic genera in which it is short and wide and the number of segments may be fixed within narrow limits. Prostomium normally with eyes and antennae. Tentacular cirri present. Parapodia uniramous or biramous, with simple and/or compound chaetae; cirri normally present. Proboscis protrusible, usually with papillae, exceptionally with chitinous jaws. Anal cirri normally present.

Representatives of two subfamilies, all members of which are exclusively pelagic, have been collected; they may be separated as follows:

1. With no antennae. Two pairs of tentacular cirri. Proboscis may have chitinous jaws. Chaetae always compound . . . . Iospilinae
2. With four antennae. Two or three pairs of tentacular cirri. Proboscis never with chitinous jaws. Chaetae compound and simple . . . Lopadorhynchinae

Subfamily Lopadorhynchinae

Key to Genera

1. Anterior parapodia modified dividing the chaetigers into two distinct regions (Text-fig. 21) . . . . *LOPADORHYNCHUS*
–. Anterior parapodia not modified 2
2. With four pairs of tentacular cirri (Text-fig. 23 . . . . . . *MAUPASIA*
–. With two pairs of tentacular cirri (Text-figs. 22 and 25) 3
3. Tentacular cirri with chaetae (Text-fig. 22) . . . . *PELAGOBIA*
–. Tentacular cirri without chaetae (Text-fig. 25) . . . . . . *PEDINOSOMA*

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[1] In 1959 Dr. R. P. Dales sought my opinion about some specimens he had from the Malacca Straits which were identical with material I had already identified from the Scripps Collections as *Travisiopsis dubia*. Dr. Dales' paper was published whilst this present work was in manuscript (see Dales, 1960).

Genus ***LOPADORHYNCHUS*** Grube, 1855

(Emended Malaquin & Dehorne, 1907 pro *Lopadorrhynchus* Grube, 1855)

Prostomium with four antennae, two dorsal, which appear as anterior extensions of the lateral border, and two ventral, close to the mouth. Three pairs of tentacular cirri. Parapodia uniramous and modified anteriorly so that the chaetigers are divided into two distinct regions; simple and compound chaetae are present supported by a prominent pedal lobe with acicula. Dorsal cirri present on all parapodia, ventral cirri may be absent on anterior feet. Proboscis smooth or papillate.

Type species. *Lopadorhynchus brevis* Grube, 1855.

Type locality. Mediterranean.

I have given elsewhere (Tebble, 1960) my reasons for not accepting the division of this genus into the subgenera *Lopadorhynchus sensu stricto* and *Prolopadorhynchus*.

Key to Species

1. The first three parapodia modified; with simple chaetae only and no ventral cirri **_L. brevis_**

–. The first two parapodia modified: no ventral cirri 2

2. The first two parapodia robust and stout, with strong unidentate hooks, surrounded by a " ruff ", or collar . . . . **_L. uncinatus_**

. The first two parapodia not robust or stout; with simple unidentate hooks, without a ruff or collar . . . . **_L. krohnii_**

Lopadorhynchus brevis Grube, 1855

Lopadorrhynchus brevis Grube, 1855, p. 100, pl. 3, fig. 15.
Lopadorrhynchus parvum Chamberlin, 1919, pp. 114–116, pl. 17, figs. 6, 7.
Lopadorhynchus brevis: Fauvel, 1923, p. 184, fig. 69*k*.
Lopadorhynchus (*Lopadorhynchus*) *brevis*: Dales, 1957, pp. 104–105, figs. 7–8.
Lopadorhynchus brevis: Tebble, 1960, pp. 200–201; pp. 259–261, fig. 52.

Description. The largest specimen collected measures 7 mm. in length for twenty-two chaetigers and the smallest 2·5 mm. for sixteen. The parapodia are divided into two separate regions at the posterior border of the third chaetiger. The prostomium is wider than long, with a straight anterior border with two long dorsal and two ventral antennae. Two eyes may be present but are not always clearly visible. There are three pairs of tentacular cirri, one dorsal and one ventral just behind the antennae and the third very small almost an appendage of the lower of these. The first three parapodia have no ventral cirri; up to seven stout simple chaetae project, fan-wise, from a spatulate pedal lobe. Thereafter, compound chaetae, with oval terminal pieces on a pronounced heterogomph articulating surface, appear on all feet, with simple chaetae grouped ventrally becoming less numerous. On the fourth chaetiger there may be five to eight simple chaetae but on far posterior feet there may be none or only one. Dorsal cirri are foliaceous, ventral cirri smaller and subulate.

Discussion. The largest of the specimens reported here is smaller than those reported by Dales (1957) from the California Current, which measure up to 17 mm. in length, or by Tebble (1960) from the South Atlantic which reach 20 mm. in length. They differ from these also in other characters which would normally be associated with differences in stages of growth ; chaetae are neither as large nor so numerous, cirri are less well formed, and there are fewer chaetigers.

In my *Discovery* report (Tebble, 1960) I suggested that *L. nans* Chamberlin, 1919, was synonymous with *L. brevis* although Støp-Bowitz (1948) suggested it might be a synonym of *L. nationalis* Reibisch, 1895. In July, 1959, I examined the type specimen of *L. nans* in the Smithsonian Institution, Washington, U.S.N.M. No. 19402, and found it in poor condition and am unable to confirm either my own or Støp-Bowitz's opinion. At the same time I examined the type specimen of *L. parvum* Chamberlin, 1919, U.S.N.M. No. 19403 and found it similar to *L. brevis*.

General distribution. *L. brevis* is known only from Tropical and Sub-Tropical waters (see below, pp. 463, 465).

Lopadorhynchus uncinatus Fauvel, 1915

Original localities. From off the Azores and Monaco.

Lopadorhynchus uncinatus Fauvel, 1915, p. 3, fig. 2.
Lopadorhynchus uncinatus : Fauvel, 1923, pp. 184–185, fig. 67, *a–g*.
Lopadorhynchus varius Treadwell, 1943, pp. 32–33, pl. 1, figs. 7–10.
Lopadorhynchus (*Lopadorhynchus*) *uncinatus :* Støp-Bowitz, 1948, pp. 17–18, fig. 11.
Lopadorhynchus (*Lopadorhynchus*) *uncinatus :* Dales, 1957, pp. 101–104, figs. 1–6.
Lopadorhynchus uncinatus : Tebble, 1960, p. 201 ; pp. 259–261, fig. 52.

Description. The largest specimen measures 21 mm. in length for twenty-six chaetigers and the smallest 6 mm. for twenty-four. The parapodia are divided into two separate regions at the posterior border of the second chaetiger. The prostomium is wider than long, pointed anteriorly with two long dorsal and two short ventral antennae. Two eyes may be present but they are not always clearly visible. The first two tentacular cirri are long and cirriform lying dorsally and ventrally just behind the antennae, the third is very small and subulate, situated on the ceratophore which supports the ventral pair. The first two parapodia are much more prominant than the rest, they are large, stout, and directed laterally, with up to seven strong unidentate simple hooks, surrounded by a ruff or collar and with a small dorsal cirrus but no true ventral cirrus. The succeeding feet are thin and paddle-shaped, and directed backwards, with chaetae grouped fan-wise about the pedal lobe. From the third parapodia both simple and compound chaetae are present but the latter gradually replace the former. The terminal article of the compound chaetae is ovate with serrations on one side ; the articulation is heterogomph. Dorsal cirri are short and conical, ventral cirri are smaller and subulate.

Discussion. As Dales (1957) notes *L. varius* Treadwell, 1943, is almost certainly synonymous with *L. uncinatus*.

General distribution. *L. uncinatus* is known only from Tropical and Subtropical waters (see below, pp. 463, 465).

Lopadorhynchus krohnii (Claparède), 1870*

(Text-fig. 21)

Type locality. Naples.

Hydrophanes krohnii Claparède, 1870, pp. 464–466, pl. 11, fig. 2.
Lopadorhynchus krohnii : Fauvel, 1923, pp. 185–186, fig. 69*a–d*.
Lopadorhynchus (*Lopadorhynchus*) *krohnii :* Dales, 1957, pp. 105–106, figs. 9, 10.
Lopadorhynchus krohnii : Tebble, 1960, p. 202 ; pp. 259–261, fig. 52.

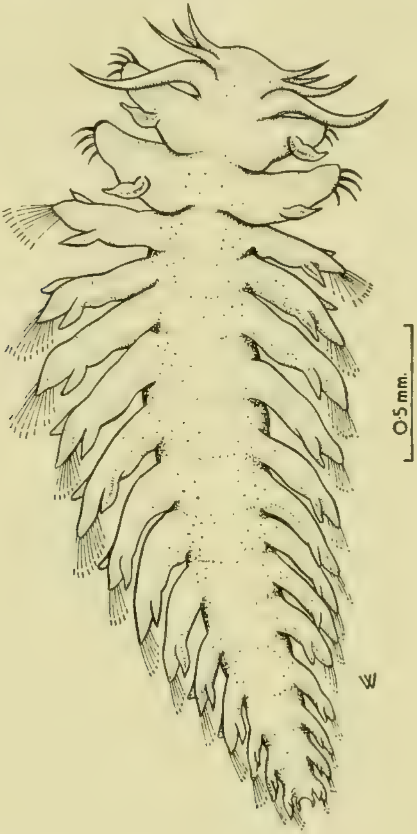

FIG. 21. *Lopadorhynchus krohnii :* specimen from Stn. 123A of the Trans-Pacific Exp.

DESCRIPTION. The largest specimen collected measures 9 mm. in length for twenty chaetigers and the smallest 1·5 mm. for eleven. The parapodia are divided into two distinct regions at the posterior border of the second chaetiger. The

* See Addenda, p. 492.

prostomium is twice as wide as long, with a rounded anterior border and two long dorsal and two short ventral antennae. No eyes are visible in any of the specimens. There are two long, dorsal and ventral pairs of tentacular cirri, and on the ceratophore at the base of the ventral pair there is a minute pimple, which must be regarded as a third tentacular cirrus. The first two chaetigers are directed laterally and are shorter and stouter than the rest; they have simple hooked chaetae and a dorsal cirrus but no ventral cirrus. The remaining parapodia are directed posteriorly and are thin and paddle-shaped with small dorsal and ventral cirri; chaetae are compound, with heterogomph articulation and serrated ovate terminal pieces, grouped fan-wise about the pedal lobe.

DISCUSSION. This description differs from that in all previous descriptions of this species in noting the presence of a minute third tentacular cirrus. In re-examining the specimens of *L. krohnii* reported in Tebble (1960) from the South Atlantic I see that these also have this organ, as do those reported by Dales (1957), from the California Current, and material in the University Museum, Copenhagen from the North Atlantic.

GENERAL DISTRIBUTION. *L. krohnii* is known only from Tropical and Sub-Tropical waters (see below, pp. 463, 464).

Genus ***PELAGOBIA*** Greeff, 1879

Prostomium with four antennae. Two pairs of tentacular cirri with chaetae. Parapodia uniramous with dorsal and ventral cirri cylindrical (dorsal cirrus reduced or absent on the second chaetiger) and compound chaetae. Proboscis smooth. Pygidium with two cirri.

Type species. *Pelagobia longicirrata* Greeff, 1879.

Type locality. Arrecife, Canary Islands.

Pelagobia longicirrata Greeff, 1879

(Text-fig. 22)

Pelagobia longicirrata Greeff, 1879, pp. 247–249, pl. 14, figs. 23–25.
Pelagobia longicirrata: Fauvel, 1923, p. 192, fig. 72, *a*, *c*.
Pelagobia longicirrata: Støp-Bowitz, 1948, p. 21.
Pelagobia longicirrata: Uschakov, 1957*a*, p. 268, Chart 1.
Pelagobia longicirrata: Dales, 1957, pp. 107–108, figs. 11–13.
Pelagobia longicirrata: Tebble, 1960, pp. 202–204; pp. 237–242, figs. 37–44, Tables 18, 19.

DESCRIPTION. This species measures up to 12 mm. in length for fifteen to thirty chaetigers. The prostomium is approximately cone-shaped, truncated anteriorly, with two eyes and four small antennae. At the lateral posterior corners of the prostomium there are two shoulders which may carry numerous pigmented spots. The two pairs of tentacular cirri are long and subulate, between each is a pedal mamelon with compound chaetae. There is a ventral cirrus but no dorsal cirrus on the second chaetiger (counting the segment carrying the tentacular cirri as the first chaetiger). Thereafter parapodia have long cylindrical dorsal and ventral cirri. All chaetae are compound with smooth shafts but the terminal articles are denticulated along one edge. Anal cirri are short and blunt.

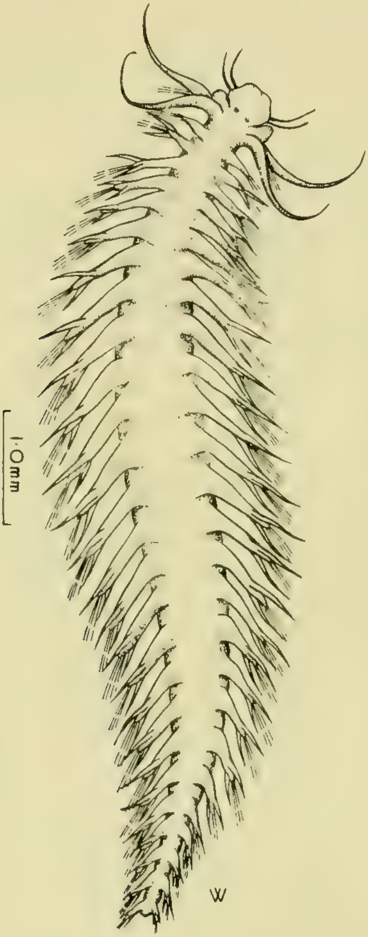

FIG. 22. *Pelagobia longicirrata* : specimen from Stn. 42E of the Trans-Pacific Exp.

GENERAL DISTRIBUTION. *P. longicirrata* is known from almost all explored water masses throughout the world (see below, pp. 460, 462).

Genus ***MAUPASIA*** Viguier, 1886

Prostomium with four antennae. Four pairs of tentacular cirri. Parapodia uniramous with dorsal and ventral cirri and compound chaetae only. Proboscis smooth.

Type species. *Maupasia caeca* Viguier, 1886.

Type locality. Bay of Algiers.

Maupasia caeca Viguier, 1886

(Text-figs. 23, 24)

Maupasia caeca Viguier, 1886, pp. 382–385, pl. 21, figs. 14–20.
Maupasia caeca : Fauvel, 1923, pp. 190–191, fig. 171*a–d*.
Maupasia caeca : Uschakov, 1957*a*, pp. 268–269, Chart 1, fig. 1, *c–e*.
Maupasia caeca : Tebble, 1960, pp. 204–205 ; p. 242, fig. 44.

DESCRIPTION. The largest specimen collected measures 7·5 mm. in length for twenty chaetigers and the smallest 2 mm. for twelve (in these counts the segments carrying the tentacular cirri, which always bear chaetae, have been counted as chaetigers). The prostomium is as wide as long and carries two dorsal and two ventral antennae. There are four pairs of tentacular cirri arranged thus, 1/1 + 1/1, on successive segments behind the head. The anterior pairs are pointed and as long as the width of the prostomium ; the posterior dorsals are almost twice as long as these and the posterior ventrals about the same length or a little smaller. Groups of compound chaetae project from between each pair of tentacular cirri. Immediately in front of the tentacular cirri, but behind the antennae, a group of cirriform vibratile organs may be visible. These are retractile and may not always be protruding but the pit from which they emerge can always be detected. The first true parapodia appear immediately behind the tentacular cirri. On all parapodia dorsal cirri are cordiform with an extended tip or as Viguier (1886) described them " en forme de coeur irregulier " ; ventral cirri are elongate and the pedal lobes lanceolate but all cirri may become swollen and mis-shaped in appearance in specimens carrying eggs. All chaetae are compound with a pronounced heterogomph articulation.

DISCUSSION. The method of counting tentacular cirri in this genus needs clarification, for which comparison with other polychaetes is necessary. Considering the definition of *Nereis* by Fauvel (1923 : 328), this genus has altogether eight tentacular cirri, four on each side of the peristomium, that is, four pairs. This is universally accepted today and the same method of counting is applied to all families of Polychaeta. Fauvel (1923) in defining *Maupasia*, however, notes that it has three pairs of tentacular cirri and therefore we would expect it to have six altogether, three on each side, but, in fact, from Fauvel's description of *M. caeca*, it appears to have twelve altogether ; that is, six pairs and not three. Fauvel (1923) takes this count from Viguier's (1886) original description, which was prepared before a common method of counting tentacular cirri was adopted. I explain below, however, why

M. caeca has, in fact four pairs of tentacular cirri (equivalent to two pairs in Fauvel's description) and not six pairs (equivalent to the three pairs in Fauvel's account).

Since Viguier's original account of *M. caeca* all authorities have accepted that this species has three pairs of tentacular cirri on each side of the body, i.e., twelve altogether. In reading Viguier's account, however, it is clear that he counted the first pair of parapodial cirri as a third pair of tentacular cirri on each side. Furthermore, Viguier's original figure (1886, pl. xxi, fig. 15) shows only two pairs on each side, i.e., eight altogether, although the presence of vibratile organs may have confused the issue. It is singular that Fauvel does not mention these vibratile organs because his figure, which was taken directly from Viguier's work, shows them. Fauvel, however, would certainly not mistake parapodial cirri for tentacular cirri and I think he got his third pair of tentacular cirri on each side by counting a pair of the vibratile organs. Occasionally only one of these protrudes on either side (although

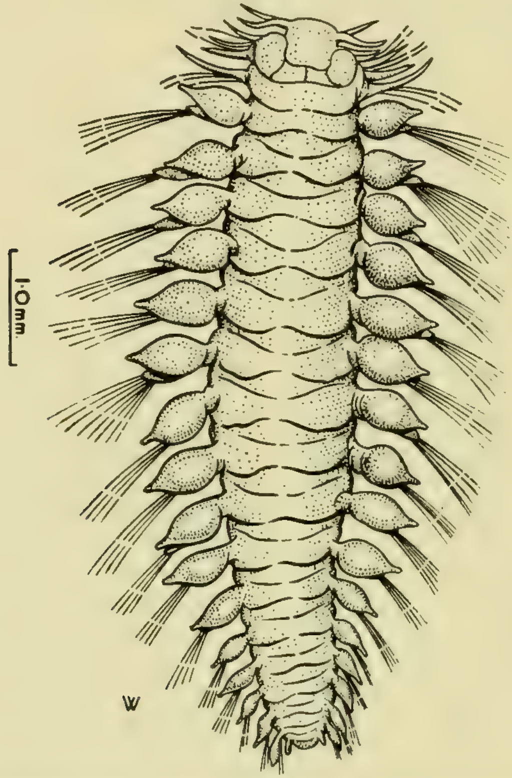

FIG. 23. *Maupasia caeca* : Specimen from Stn. 27B of the Trans-Pacific Exp.

there may be up to eight showing sometimes) and if so they answer perfectly to Fauvel's description of the most anterior pair of tentacular cirri in *Maupasia* thus : " une dorsal et une ventrale sur le premier segment, soude au prostomium et pourvu d'acicules et de soies ".

In making this correction to the definition of *M. caeca* I have examined material from the North Atlantic in the collections of the University Museum, Copenhagen, and that reported from the southern hemisphere by Ehlers (1912), Benham (1927), Hardy & Gunther (1935) and Tebble (1960).

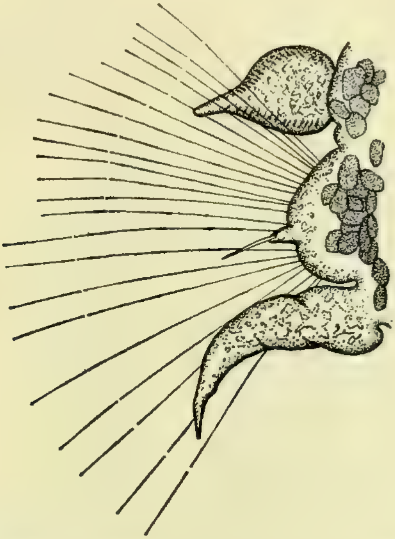

FIG. 24. *Maupasia caeca :* parapodium from the sixth chaetiger of specimen from Stn. 34B of the Trans-Pacific Exp.

GENERAL DISTRIBUTION. The first records of *M. caeca* from the North Pacific were made recently by Uschakov (1957*a*), at 48° 08′ N., 156° 08′ E. and Berkeley & Berkeley (1958) from 1° 58′ N., 83° 49′ W. Elsewhere in the world it has been recorded from scattered localities (see below, pp. 463, 466–467).

Genus ***PEDINOSOMA*** Reibisch, 1895

Prostomium with four antennae. Two pairs of tentacular cirri, without chaetae between them. Parapodia uniramous with round to ovate dorsal cirri and cylindrical ventral cirri and compound chaetae only. Proboscis smooth.

Type species. *Pedinosoma curtum* Reibisch, 1895.

Original localities. Tropical South Atlantic and Tropical and Sub-Tropical North Atlantic Oceans.

Pedinosoma curtum Reibisch, 1895

(Text-figs. 25, 26)

Pedinosoma curtum Reibisch, 1895, p. 21; pp. 27–30, pl. II, fig. 17; pl. III, figs. 1–4.
Pedinosoma curtum: Fauvel, 1923, pp. 188–189, fig. 70, *c–f*.

Description. The largest specimen collected measures 3·0 mm. long for eight chaetigers, this is a mature female, the body cavity being filled with eggs; the smallest is 1·0 mm. in length for seven chaetigers. The prostomium is a little wider than long with two pairs of thin and pointed antennae projecting laterally from the anterior lateral corner. There are two pairs of tentacular cirri, all a little longer than the body width and finely pointed: no chaetae are associated with these. Of the thirteen specimens reported here all have eight chaetigers except two, which have seven. Parapodia have round to ovate dorsal cirri and finely pointed cylindrical

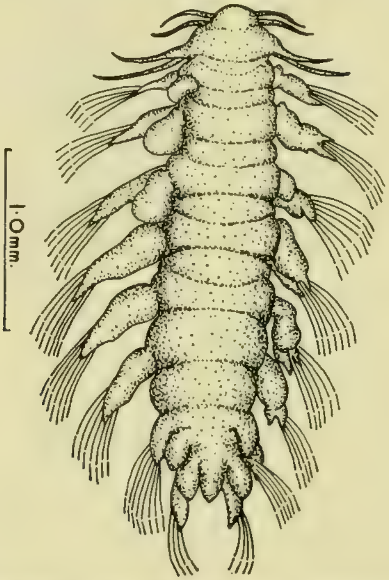

Fig. 25. *Pedinosoma curtum:* specimen from Stn. 49 of the Northern Holiday Exp. (the dorsal cirri have fallen off some segments).

ventral cirri ; pedal lobes are lanceolate and carry a large number of compound chaetae, in which the articulation is heterogomph.

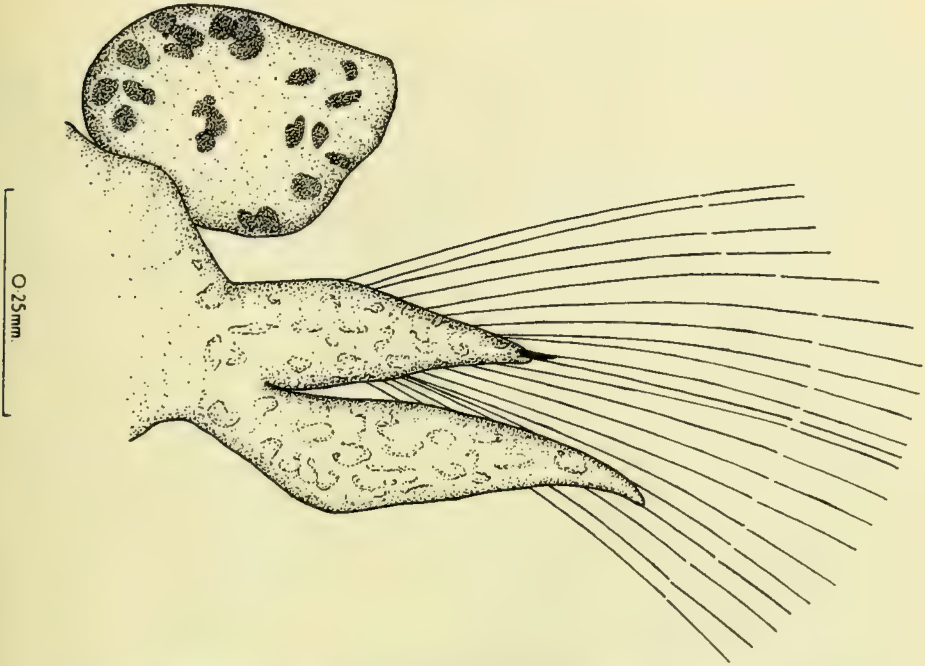

FIG. 26. *Pedinosoma curtum :* parapodium from the fourth chaetiger of specimen from Stn. 8 of the Northern Holiday Exp.

GENERAL DISTRIBUTION. This appears to be the first record of this species from the Pacific Ocean (see below, pp. 466, 467) ; it is known only from Tropical and Sub-Tropical waters in the Atlantic.

Subfamily IOSPILINAE

Genus ***PHALACROPHORUS*** Greeff, 1879

No antennae. Two pairs of tentacular cirri, of which the posterior carries chaetae. Parapodia uniramous, dorsal and ventral cirri small, compound chaetae with smooth terminal articles. Proboscis with two long chitinous teeth.

Type species. *Phalacrophorus pictus* Greeff, 1879.

Type locality. Canary Islands, Atlantic Ocean.

Phalacrophorus pictus Greeff, 1879

(Text-fig. 27*c*)

Phalacrophorus pictus Greeff, 1879, p. 249, pl. 14, figs. 25–30.
Phalacrophorus pictus: Reibisch, 1895, pp. 10–12, pl. 1, figs. 4–7.
Phalacrophorus borealis Reibisch, 1895, pp. 12–13, pl. 1, figs. 8–9.
Phalacrophorus pictus: Fauvel, 1923, p. 196, fig. 72*f*.
Phalacrophorus maculatus Treadwell, 1943, p. 34, pl. 1, figs. 11–13.
Phalacrophorus pictus: Uschakov, 1957*a*, pp. 274–275, fig. 1.
Phalacrophorus pictus: Hartman, 1956, p. 276.

Description. No complete specimens of this species were collected; the largest fragment measures 7 mm. in length for thirty chaetigers. The prostomium is bluntly rounded with no eyes visible in any of the specimens. The proboscis carries two chitinous unidentate teeth. The segmentation of the first three segments is indistinct and, when the proboscis is not everted, this part of the body is swollen. The first pair of tentacular cirri is very small and achaetous, the second longer, with a few associated chaetae. This chaetiger and the next two are poorly developed but thereafter fully developed parapodia occur, with small bulbous dorsal cirri, smaller ventral cirri, and with prominently projecting pedal lobes carrying bundles of compound capillary chaetae. These chaetae have long finely pointed terminal articles. A number of specimens have the body cavity filled with eggs.

Discussion. These specimens differ from typical *P. pictus* in being without eyes and are thus close to *P. borealis* Reibisch, 1895; this is the only difference between these species and I do not consider that it merits separating them. In all other essentials this material is identical with two specimens of *P. pictus* in the B.M. (N.H.) collections, one reported by Fauvel (1916) from the Canaries and the other identified by Monro from *Discovery* collections, " William Scoresby ", Stn. 63, near South Georgia, but not previously reported.

General distribution. *P. pictus* is known from localities scattered thoughout the world, but it is possible that a separate population inhabits sub-arctic and arctic waters of the Pacific and Atlantic Oceans (see below, pp. 466, 468–9).

Phalacrophorus uniformis Reibisch, 1895

(Text-figs. 27*a*, *b*)

Original localities. Tropical South Atlantic and Tropical and Sub-Tropical North Atlantic.

Phalacrophorus uniformis Reibisch, 1895, pp. 15–17, pl. 1, figs. 10–16.
Phalacrophorus uniformis: Fauvel, 1923, pp. 196–197, fig. 72, *g*, *h*.
Phalacrophorus attenuatus Treadwell, 1943, p. 34, fig. 14.
Phalacrophorus uniformis: Hartman, 1956, p. 276.

Description. Only fragments of this species were collected, the longest measuring 4 mm. for about sixty chaetigers. The prostomium is bluntly rounded and has

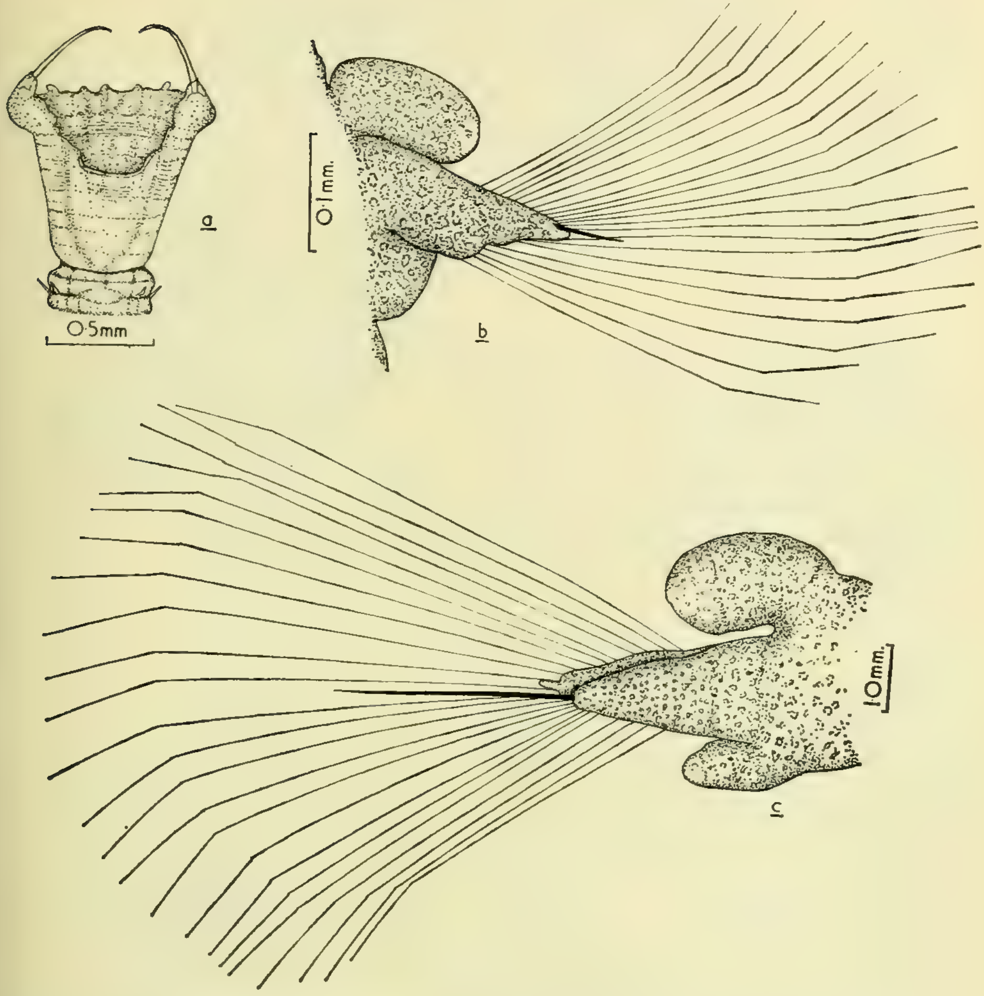

FIG. 27. *Phalacrophorus* : (*a*) *P. uniformis*, extruded proboscis of specimen from Stn. 126B of the Trans-Pacific Exp., (*b*) the same specimen, parapodium from the 128th chaetiger ; (*c*) *P. pictus* parapodium from the twelfth chaetiger of specimen from Stn. 37B.

two small brown eye spots posteriorly. The proboscis carries two chitinous unidentate teeth. The segmentation of anterior segments is distinct on the dorsal surface but tends to be hidden ventrally. The first pair of tentacular cirri is small and the second longer, bearing a few chaetae. Thereafter the first eight to twelve chaetigers are poorly developed with very few, small compound chaetae and much reduced cirri, but succeeding parapodia have very long chaetae and better developed cirri.

DISCUSSION. Hartman (1956) has examined the type specimen of *P. attenuatus* Treadwell, 1943, and considers it agrees with *P. uniformis* in important characters.

GENERAL DISTRIBUTION. *P. uniformis* is known from only a few scattered localities in the Pacific Ocean (see below, pp. 466, 468) but is well known in the Tropical and Sub-Tropical waters of the North Atlantic.

DISTRIBUTION

The families are examined below in the order followed in the Systematic Account, but genera and species have been arranged to meet zoogeographical considerations. Distribution maps have been prepared for all species. These generally indicate the presence or absence of a species at each station without an indication of the quantitative distribution because most pelagic polychaetes rarely occur in large enough numbers to make this necessary. *Tomopteris elegans*, *T. septentrionalis* and *Typhloscolex mülleri*, however, do occur in large and varying quantities and the relative abundance of these three species has been plotted.

TOMOPTERIDAE

Seven species of *Tomopteris* are reported here of which five, *T. elegans*, *T. planktonis*, *T. ligulata*, *T. nisseni* and *T. apsteini*, have never been collected in the Sub-Arctic Zone and it is clear that the southern boundary of this region or the southern boundary of the Transition Zone, indicates the limit of their northerly movement in the Pacific Ocean ; one species, *T. pacifica*, was collected only in the Sub-Arctic Zone and may be restricted to it ; and the remaining species *T. septentrionalis* was found in all three hydrological zones, substantiating its known cosmopolitan distribution.

T. elegans was collected at numerous stations across the Sub-Tropical Zone and was also found in the Transition Zone in the eastern region of the North Pacific (Text-fig. 28). It may be concluded therefore that this species has its northerly limit of distribution at the southern boundary of the Sub-Arctic Zone, though further collections may show that it extends farther north in the eastern region of the Transition Zone than in the western. There are no records in the literature which contradict this conclusion ; Izuka (1914) reported *T. elegans* from Sub-Tropical water off Japan, and Uschakov (1957*a*) records it from similar water between 35 and 40° N., in the region of 150° E. ; Dales (1957) notes it great abundance in the California Current. Elsewhere in the world *T. elegans* is known only from Tropical and Sub-Tropical waters.

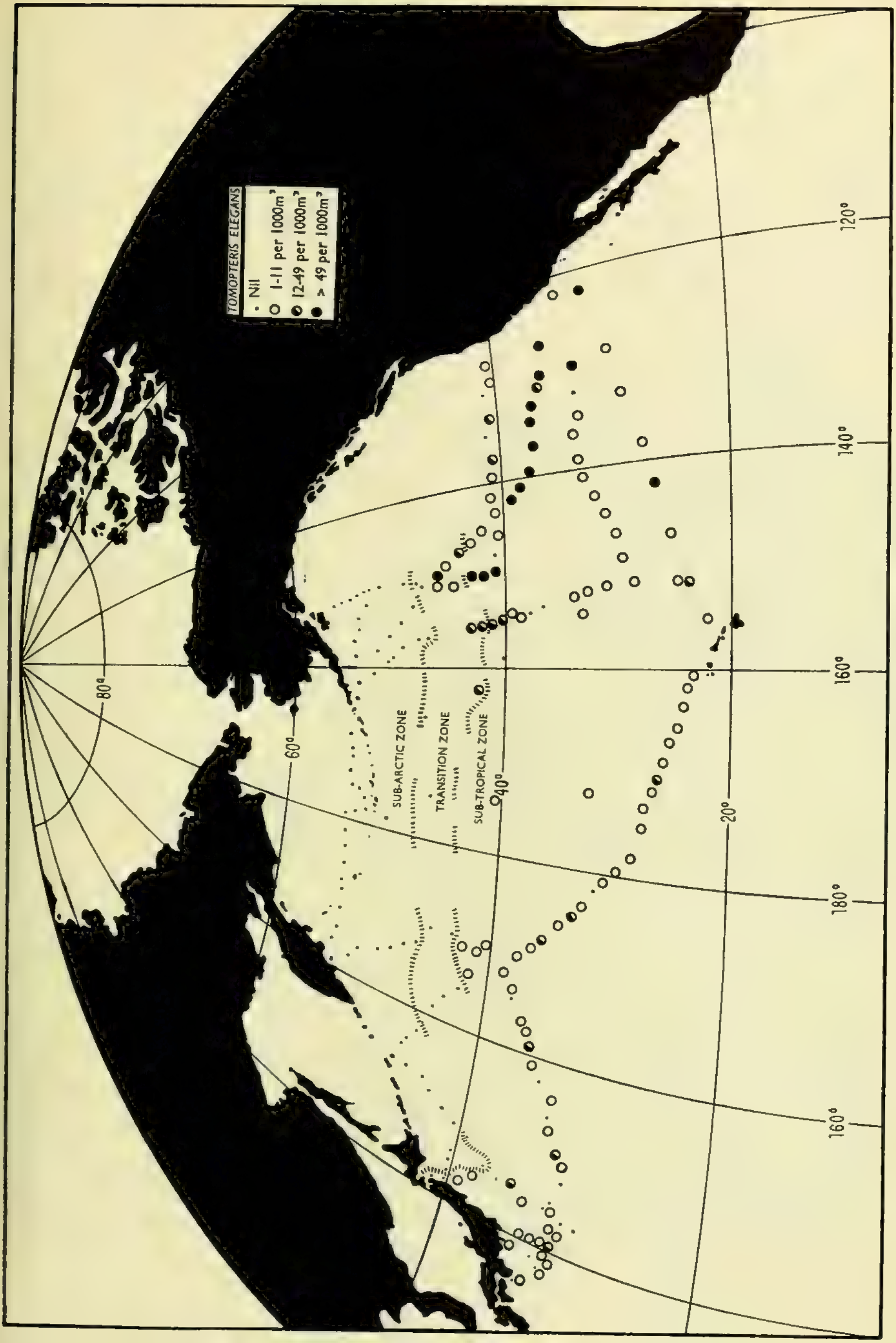
TOMOPTERIS ELEGANS
· Nil
○ 1-11 per 1000m³
◐ 12-49 per 1000m³
● > 49 per 1000m³
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 28. Occurrence of *Tomopteris elegans*.

The samples examined by Dales from the California Current were collected in the top 75 metres of water, but the Trans-Pacific Expedition explored a greater depth range in this region and its samples show that *T. elegans* occurs in abundance down to about 350 metres. Below this depth, to 680 metres, however, there is a reduction in numbers caught, to negligible quantities. *T. elegans* is evidently also more abundant in the California Current, and the area immediately to the west, than elsewhere in the North Pacific. Across the breadth of the ocean it occurred regularly, though never in great abundance, in the North Pacific Central Water Mass down to 350 metres. Below this depth it was absent from all closing nets.

There is probably a significant relationship between the distribution of *T. elegans* and *T. septentrionalis* in the eastern North Pacific, including the California Current ; this is discussed below.

T. septentrionalis was collected in all three hydrological regions occurring in greatest abundance in the Sub-Arctic Zone (Text-fig. 29). It was caught regularly in the Sub-Arctic Water Mass down to about 400 metres but rarely occurred below this depth. Across the Sub-Tropical Zone *T. septentrionalis* appeared infrequently and then only in the upper layers of water. The few records from this zone may be due to the poor state of preservation of some of the collections.[1]

T. septentrionalis has been widely reported from the North Pacific, from off Misaki, Japan (Izuka, 1914), from off British Columbia (Berkeley, 1924 ; Berkeley & Berkeley, 1948), from Tropical, Sub-Tropical and Sub-Arctic waters (Treadwell, 1943), from the Bering Sea, the Sea of Okhotsk, and across the Sub-Tropical and Sub-Arctic Zones (Uschakov, 1955, 1957*a*), from Monterey Bay and the California Current (Dales, 1955, 1957) and from the Gulf of Alaska (Berkeley & Berkeley, 1957). These records are from all explored depths, and, with the summaries of the distribution of *T. septentrionalis* from elsewhere in the world made by Støp-Bowitz (1948) and Tebble (1960), have established the species as cosmopolitan.

I give reasons below for suggesting that in the California Current, and adjacent areas in the eastern North Pacific, *T. elegans* and *T. septentrionalis* may be mutually exclusive. Their relative distribution at all depths at the first thirteen stations on the Trans-Pacific Expedition is shown in the bar-diagram Text-fig. 30. These stations cross through the California Current to the northern edge of the Sub-Tropical Zone. Where one of these species occurs in abundance the other appears in only negligible quantities, if at all. Except at Stn. 1, *T. elegans* is always the more abundant. If the results obtained by Dales (1957) from samples taken entirely in the top 75 metres of water in the California Current are analysed a somewhat similar picture emerges. Thus Text-fig. 31 (a combination of the essentials in Dales' figs. 53 and 54) shows only a small region where the two species occur together, at intensities of distribution varying between <100 to 50 per 1,000 m^3 for *T. elegans* and >100 to 25 per 1,000 m^3 for *T. septentrionalis*. Dales does not give details of

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[1] In tomopterids the organs most affected by poor preservation are the parapodial pinnules. If these are incomplete in *T. septentrionalis* identification is difficult. It is very probable therefore that a large number of the specimens listed as " *Tomopteris* not identifiable ", in the Appendix could have been called *T. septentrionalis* if in a better state of preservation. Other species of *Tomopteris*, within the same size range as *T. septentrionalis*, clearly must also fall within this category sometimes, but on the whole they have more readily distinguishable features and can be recognized from other parts of the body even when the pinnules are frayed.

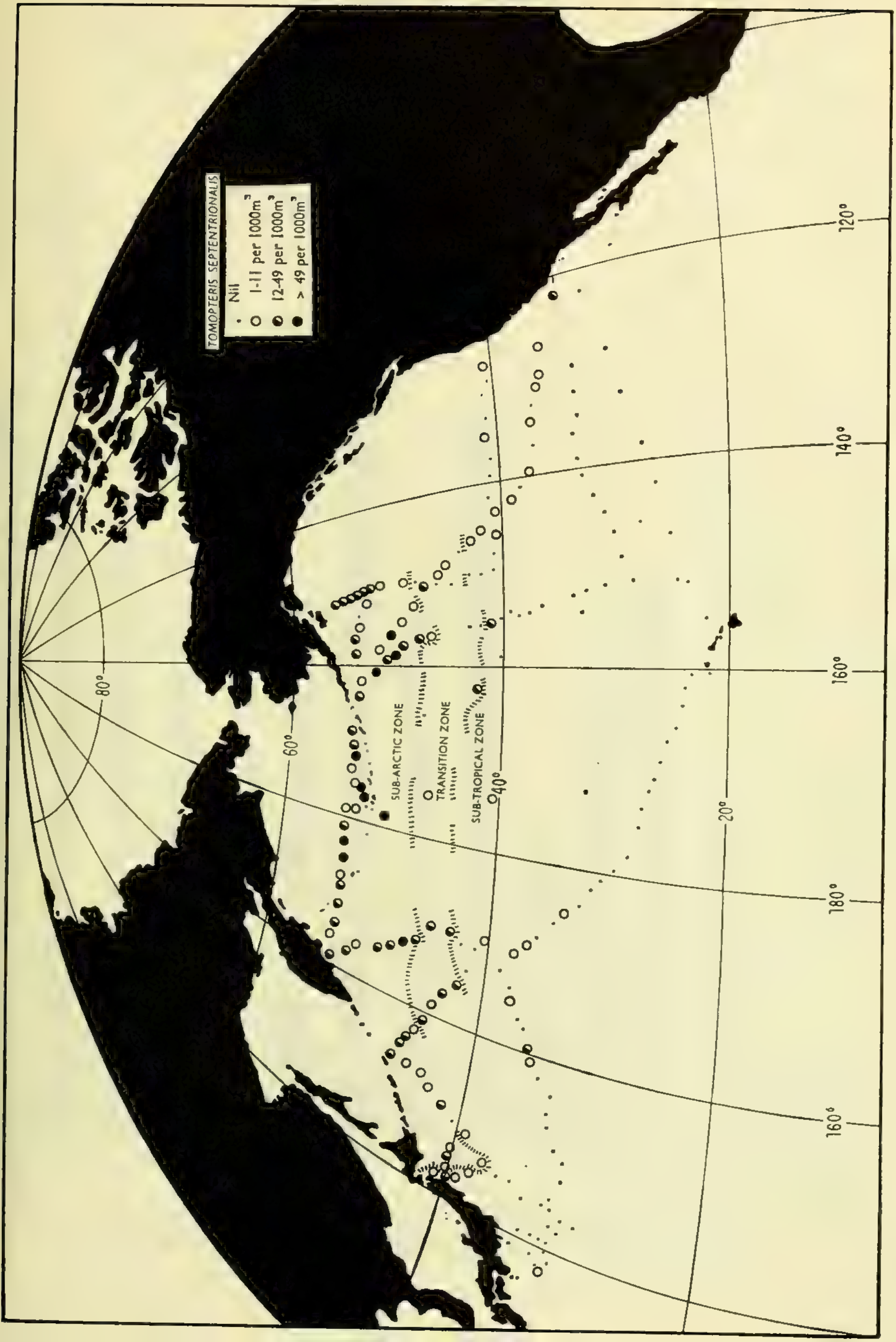
TOMOPTERIS SEPTENTRIONALIS
· Nil
○ 1-11 per 1000m³
◐ 12-49 per 1000m³
● > 49 per 1000m³
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 29. Occurrence of *Tomopteris septentrionalis.*

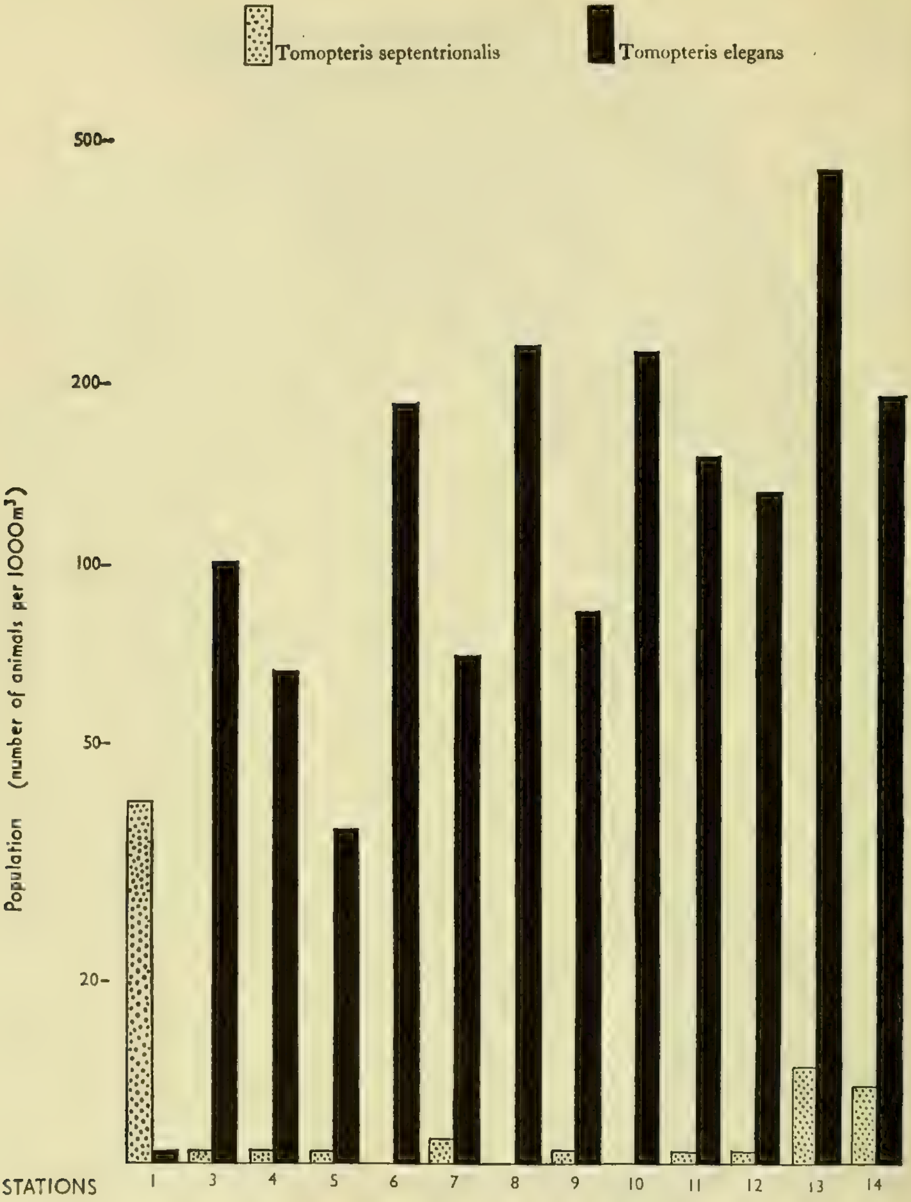

FIG. 30. Bar diagram showing the relative distribution of *T. septentrionalis* and *T. elegans* at the first thirteen stations of the Trans-Pacific Exp. (semi-log scale).

his results so that the actual number of stations where they occur together is not known but it must be small. Over the greater part of the region, and at the majority of stations, however, it is clear that where one species was collected in abundance the other was rarely present. Dales concludes from his data for *T. septentrionalis*

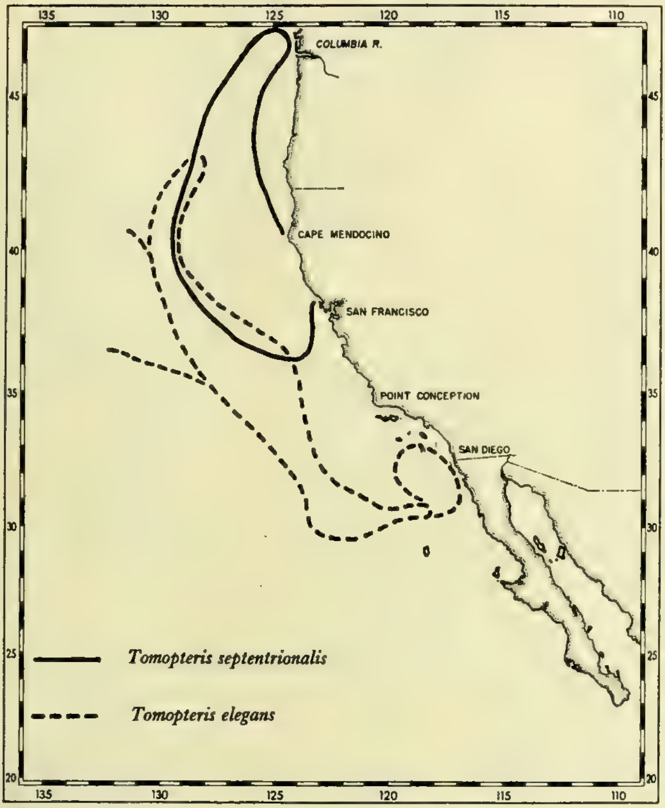
135
130
125
120
115
110
45
40
35
30
25
20
COLUMBIA R.
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
Tomopteris septentrionalis
Tomopteris elegans

FIG. 31. Occurrence of *T. septentrionalis* and *T. elegans* in the region of the California Current (adapted from Dales (1957), figs. 53 and 54).

that it is a cold water coastal form; in fact, as noted above it is cosmopolitan, having been reported from all extremes of hydrological conditions. It is possible that where *T. elegans* occurs in abundance *T. septentrionalis* does not find conditions suitable for developing large populations. Because *T. elegans* is essentially a warm water form (i.e., it is confined to Tropical and Sub-Tropical waters), *T. septentrionalis* is forced into relatively colder waters whenever conditions exist where it could exist in abundance if *T. elegans* were not present. This appears to be applicable to distribution within the California Current and possibly westward to about

145° W.,[1] but no results are available to suggest it applies over the main body of North Pacific Central Water, or elsewhere in the world.

T. planktonis was collected at numerous stations, all within the Sub-Tropical and Transition Zones (Text-fig. 32) and it is clear that in the North Pacific this species must only rarely if ever cross the northern boundary of this latter region. It appeared only in nets towed open to the surface, and in closing nets towed between 370 and 120 metres, and must be essentially an inhabitant of the upper water layers. In only two samples were more than ten specimens collected ; at one of these, from Northern Holiday Stn. 55, twenty-two were present, equivalent to twenty-eight per 1,000 m^3 of water.

Dales (1955) was the first to report *T. planktonis* from the North Pacific, recording it as *T. cavallii* from Monterey Bay ; under the same name he reported it from the California Current (Dales, 1957). Berkeley & Berkeley (1957) reported *T. cavallii* from the region of the Alaskan Gyral, about 55° N., 140° W., and although I have not examined this material it may be *T. planktonis*. Elsewhere in the world *T. planktonis* has been reported from the Antarctic by Augener (1929), Monro (1930 as *T. carpenteri*), Støp-Bowitz (1949, 1951) and Tebble (1960), from the Sub-Tropical and Tropical Atlantic by Apstein (1900), Monro (1936) and Tebble (1960) whilst Støp-Bowitz (1948) called it a bipolar species. It was expected therefore that *T. planktonis* would occur in some abundance in the North Pacific Sub-Arctic Zone, but it appears to be absent from this region, except as possibly a coastal migrant if future work shows that Berkeley & Berkeley (1957) records of *T. cavallii* are identical with the material reported here.

T. pacifica was collected only in the Sub-Arctic and Transition Zones (Text-fig. 33) and is probably restricted to colder waters in the North Pacific. It was rarely collected in abundance, normally there being only one or two specimens in a sample but ten were present in the catch made at Stn. 19B of the Trans-Pacific Expedition, equivalent to thirty per 1,000 m^3 of water. Only nets towed open to the surface and those closing between 500 and 140 metres collected *T. pacifica*, so that at the present state of our knowledge it must be considered principally an inhabitant of the upper waters.

T. pacifica has previously been reported from the Sub-Arctic Zone of the North Pacific by Berkeley (1924, as *T. elegans*), Berkeley & Berkeley (1948, 1957 and 1960, as *T. renata*) and Uschakov (1952, 1955 and 1957*a* as *T. renata*). Dales (1955) reported it from deep water in Monterey Bay, which is probably the southern limit of its distribution along the west coast of the U.S.A.—he did not find it in the California Current. If there were no reports of this species from Sub-Tropical water in the North Pacific these records would substantiate the suggestion that it is a cold water species. There is, however, one,[2] the original description of *T.*

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[1] In this region *T. elegans* may never inhabit waters north of about 45° N., and care must therefore be taken to restrict examination of this relationship to waters of which both species are known to be tolerant. In Monterey Bay, for example, Dales (1955) found *T. septentrionalis* in abundance but does not report finding any specimens of *T. elegans*.

[2] Disregarding entirely Chamberlin's (1919) species called *T. eura*, which though superficially like *T. pacifica*, and reported from the Sub-Tropical Zone, is imperfectly described and cannot at the present time be accepted as the same species (see also Dales, 1957). Consequently Treadwell's (1943) records of *T. eura* must also be disregarded because he gave no additional information.

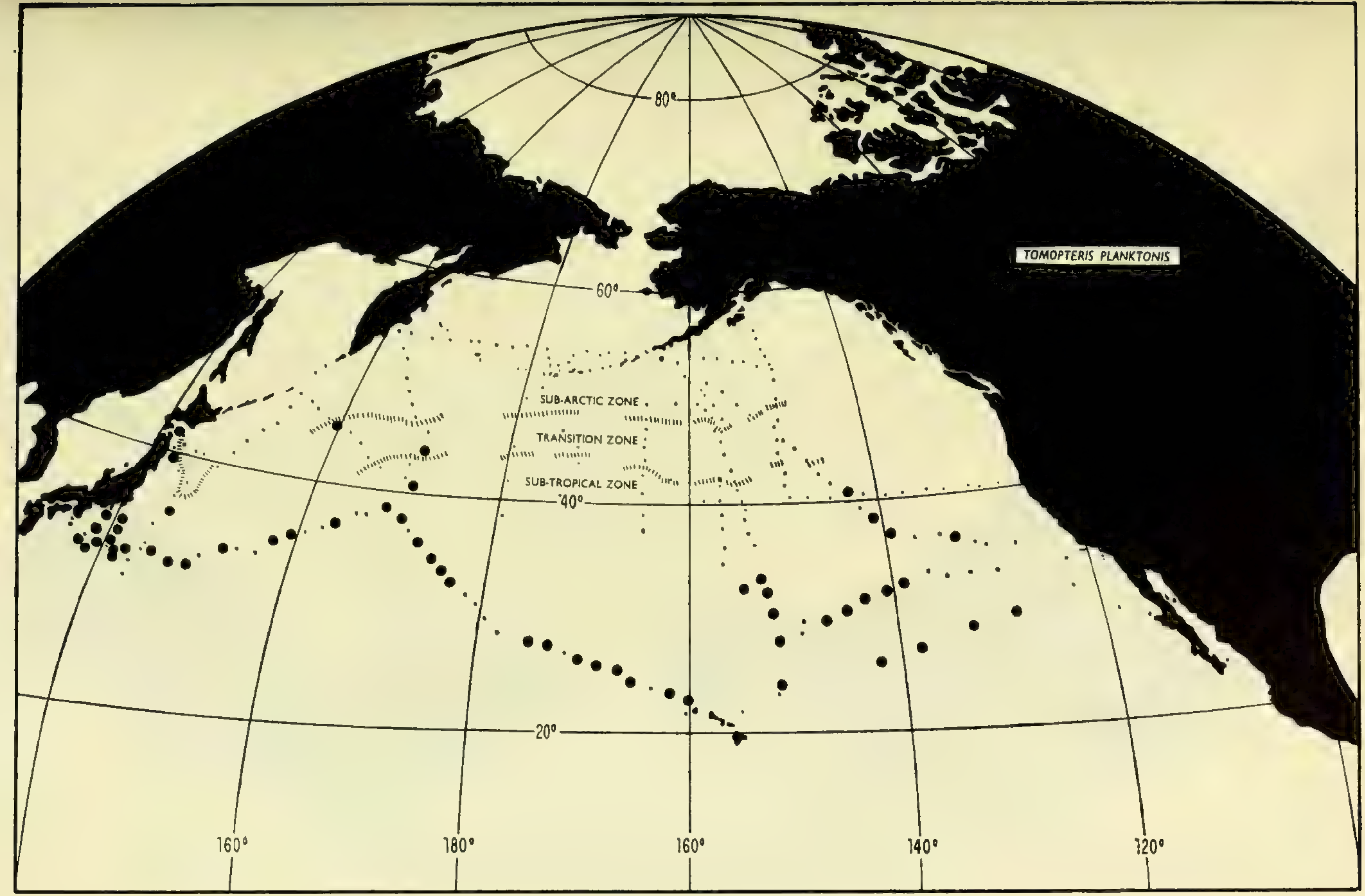
TOMOPTERIS PLANKTONIS
80°
60°
40°
20°
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
160°
180°
160°
140°
120°

FIG. 32. Occurrence of *Tomopteris planktonis*.

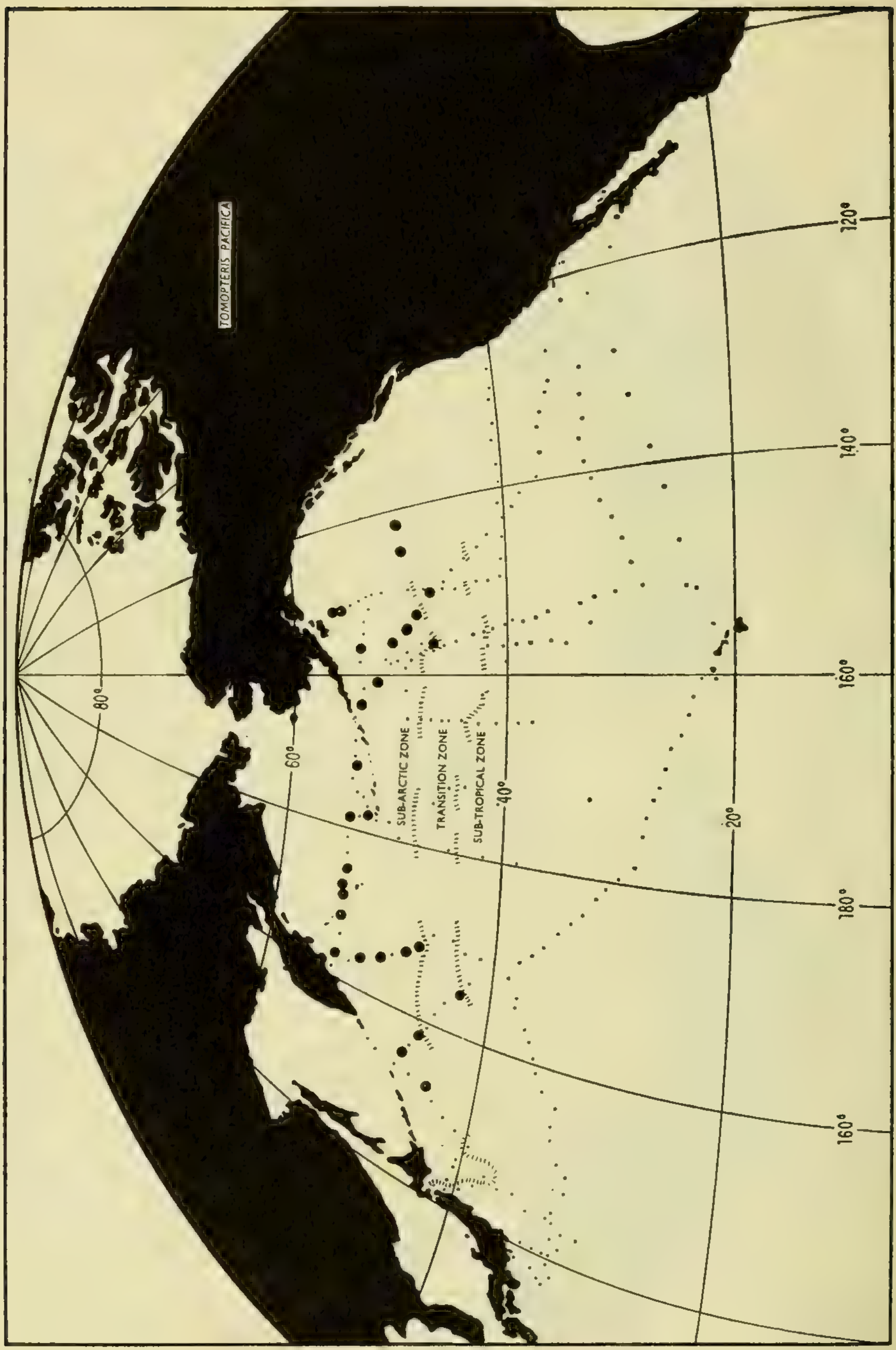
TOMOPTERIS PACIFICA
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 33. Occurrence of *Tomopteris pacifica*.

pacifica having been made by Izuka (1914) from a sample collected off Misaka, Japan, in which there were also present six undoubtedly sub-tropical species, including *T. elegans* and *T. apsteini*. Undoubtedly Izuka was describing what is accepted as the valid species, *T. pacifica*, but the absence of any other undoubted records of it since that time from the Sub-Tropical Zone suggests that his record was anomalous, possibly the product of an aberrant coastal migration. It may be unfortunate that the type locality of this species is outside the limits of its hydrological environment but this does not effect its validity and should not be used as grounds for accepting *T. renata* as its name.

T. ligulata was collected only in the Sub-Tropical Zone and it is probable that the northern boundary of this region restricts its northerly movement (Text-fig. 34). The records made here appear to be the first for the species from the North Pacific Ocean; Rosa (1908*b*) reported it from 31° S., 80° W., in the South Pacific. All catches were made in nets hauled between 370 metres and the surface, and the largest number of specimens collected was six, at Trans-Pacific Stn. 120B, equivalent to fifteen per 1,000 m^3 of water, so that this species must only rarely become numerically abundant. Elsewhere in the world *T. ligulata* is known only from Tropical and Sub-Tropical waters.

T. apsteini was not collected at many stations but, nevertheless, these were all in the Sub-Tropical Zone (Text-fig. 35) and it probably never occurs further north than this region. Very rarely was more than one specimen collected, the most being four at Stn. 56 of the Northern Holiday Expedition, equivalent to five per 1,000 m^3 of water. All collections were made in the upper 300 metres. Rosa (1908*b*) first recorded *T. apsteini* from the North Pacific, off Mexico, and Izuka (1914) reported it off Misaki, Japan. Elsewhere in the world it is also known only from Tropical and Sub-Tropical waters.

T. nisseni occurred at stations scattered across the Sub-Tropical Zone (Text-fig. 35), but was never collected beyond its northern boundary which suggests that this acts as a barrier restricting its northerly movement. Dales (1955) recorded this species from deep water in Monterey Bay which was the first undoubted record from the North Pacific. On the Trans-Pacific Expedition *T. nisseni* was caught only in the top 370 metres of water; all of these catches except two were within North Pacific Central Water. At Stns. 7A and 7C it was collected in the California Current but it appears to inhabit this water only rarely for it was not recorded in Dales' (1957) extensive survey of the area.

Elsewhere in the world, in the southern hemisphere, *T. nisseni* is known only from Tropical and Sub-Tropical waters. In the North Atlantic, however, there are valid records from boreal waters (Wesenberg-Lund, 1950) and it was expected, therefore, that it would occur in the Sub-Arctic waters of the North Pacific; this matter is discussed further, below p. 469.

ALCIOPIDAE

Twelve species within this family are reported here. All were collected at numerous stations in the Sub-Tropical Zone; a few appeared also in the Transition

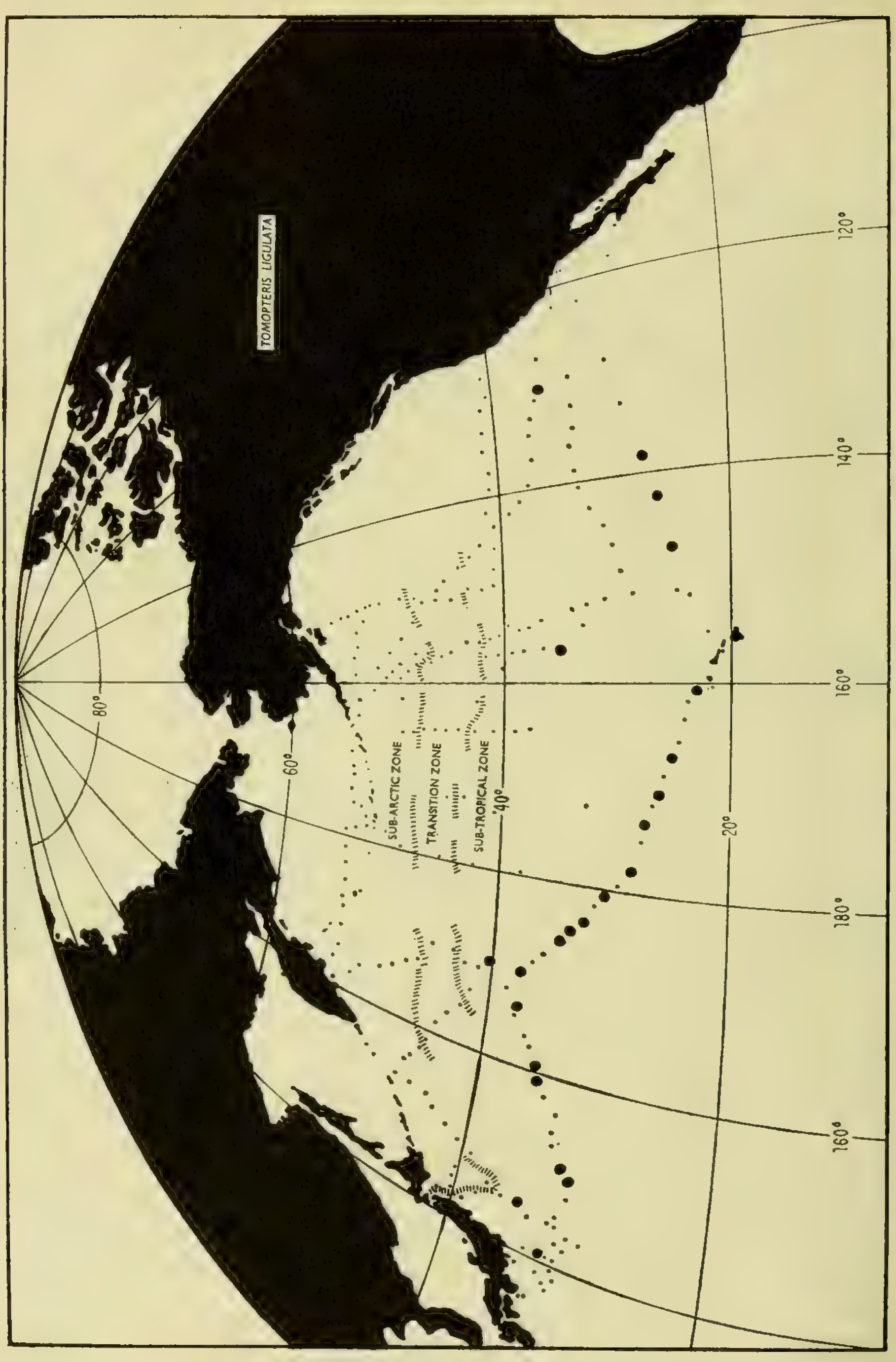
TOMOPTERIS LIGULATA
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 34. Occurrence of *Tomopteris ligulata*.

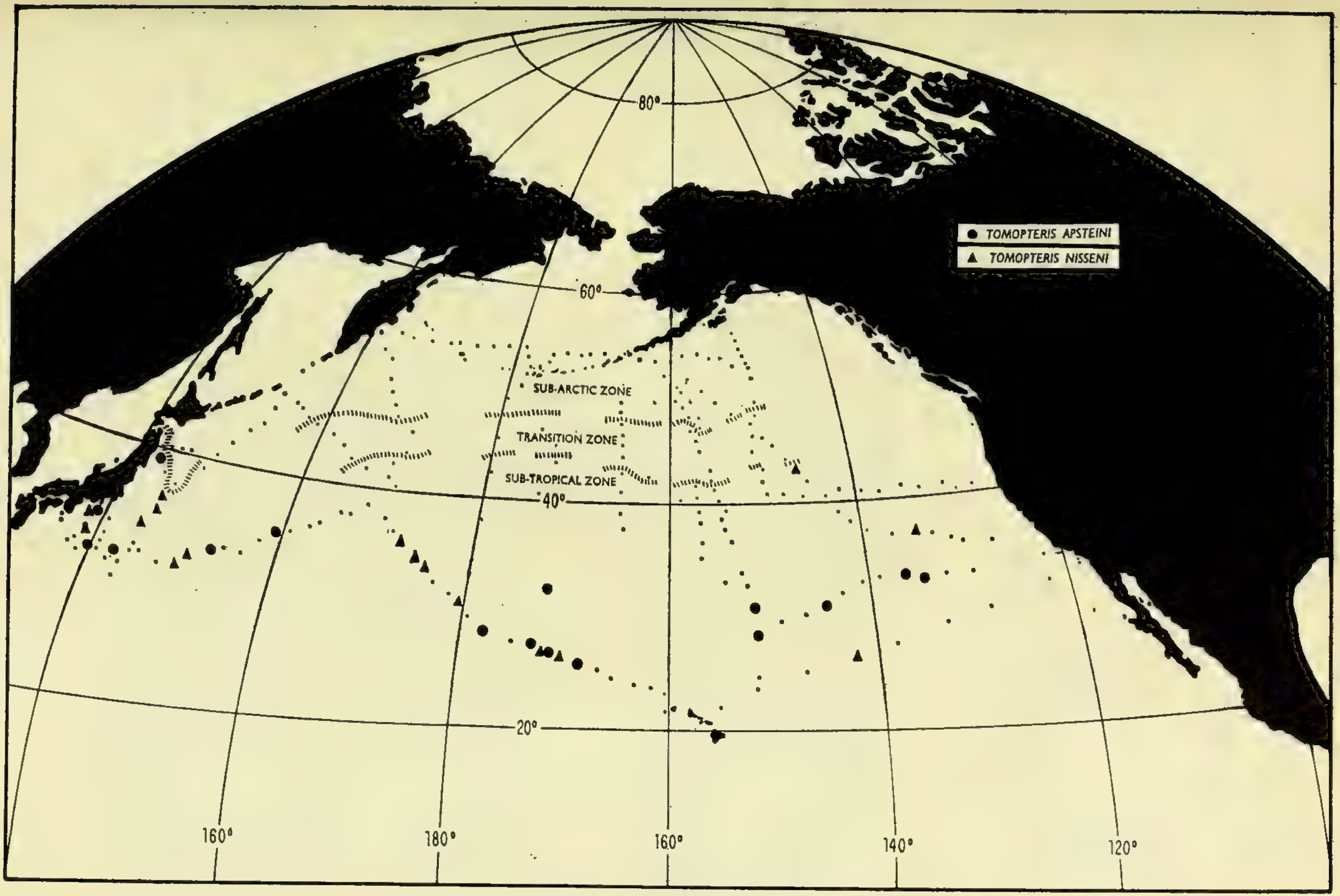
● TOMOPTERIS APSTEINI
▲ TOMOPTERIS NISSENI
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
160°
180°
160°
140°
120°

FIG. 35. Occurrence of *Tomopteris apsteini* and *T. nisseni.*

Zone but only one (*Rhynchonerella angelini*) was collected in abundance in the Sub-Arctic.

In Tables I and II of the Appendix the presence or absence of alciopid fragments (headless pieces) at each station has been indicated. This item is included because of the Zoogeographical importance of the family as a whole to which the presence or absence of these fragments lends significance. Thus many more genera and species of Alciopidae occur in the Sub-Tropical and Tropical Zones of the South Atlantic than in the waters of higher latitudes (Tebble, 1960), and this is shown below to apply also to the North Pacific. The recording of the presence of the fragments is additional proof of this. These were, for example, found at a large number of stations in the Sub-Tropical Zone (Appendix, Table I) but at very few in the Sub-Arctic (Table II); an indication that numerous species (up to twelve) can be found in the Sub-Tropical Zone and that only one permanently inhabits the Sub-Arctic.

NAIADES

Naiades cantrainii was collected at numerous stations all in the Sub-Tropical Zone (Text-fig. 36). It probably only rarely if ever occurs north of this region. Collected only by nets towed open to the surface, in the top 150 metres of water, *N. cantrainii* must here be considered a surface water species. The largest number of specimens present in any tow at which the amount of water filtered was measured, was two, at Stn. 104A, of the Trans-Pacific Expedition equivalent to five per 1,000 m^3 of water. The species was first reported from the North Pacific by Treadwell (1943 as *Alciopa distorta*), between California and Hawaii, and subsequently Dales (1957) found it in the California Current. Elsewhere in the world it is known only from Tropical and Sub-Tropical waters.

VANADIS

None of the five species of *Vanadis* reported here was collected in the Sub-Arctic Zone, and only *V. longissima* was collected in the Transition Zone (one record), so it is probable that the southern boundary of this latter region restricts their movement northwards. Elsewhere in the world all five species are known only from tropical and sub-tropical waters, except *V. longissima* which has also been reported from the sub-antarctic region of the South Atlantic (Tebble, 1960).

V. minuta was collected more often than any other alciopid, occurring regularly at stations across the breadth of the North Pacific, south of the Transition Zone (Text-fig. 37), and it clearly never penetrates north of the southern boundary of this region. It is evidently a surface water species for it was present in thirty-eight hauls towed open to the surface from 190 m., or less, but by only two nets closing at sub-surface depths (at Trans-Pacific Expedition Stns. 132B, 345–153 m. and 135B, 290–146 m.) and never appeared in nets closed at greater depths. The largest number collected was nine at Stn. 123A, equivalent to eighteen per 1,000 m^3 of water filtered, but normally the numbers were smaller than this and it may be presumed that *V. minuta* only rarely occurs in abundance. Treadwell's (1906) type

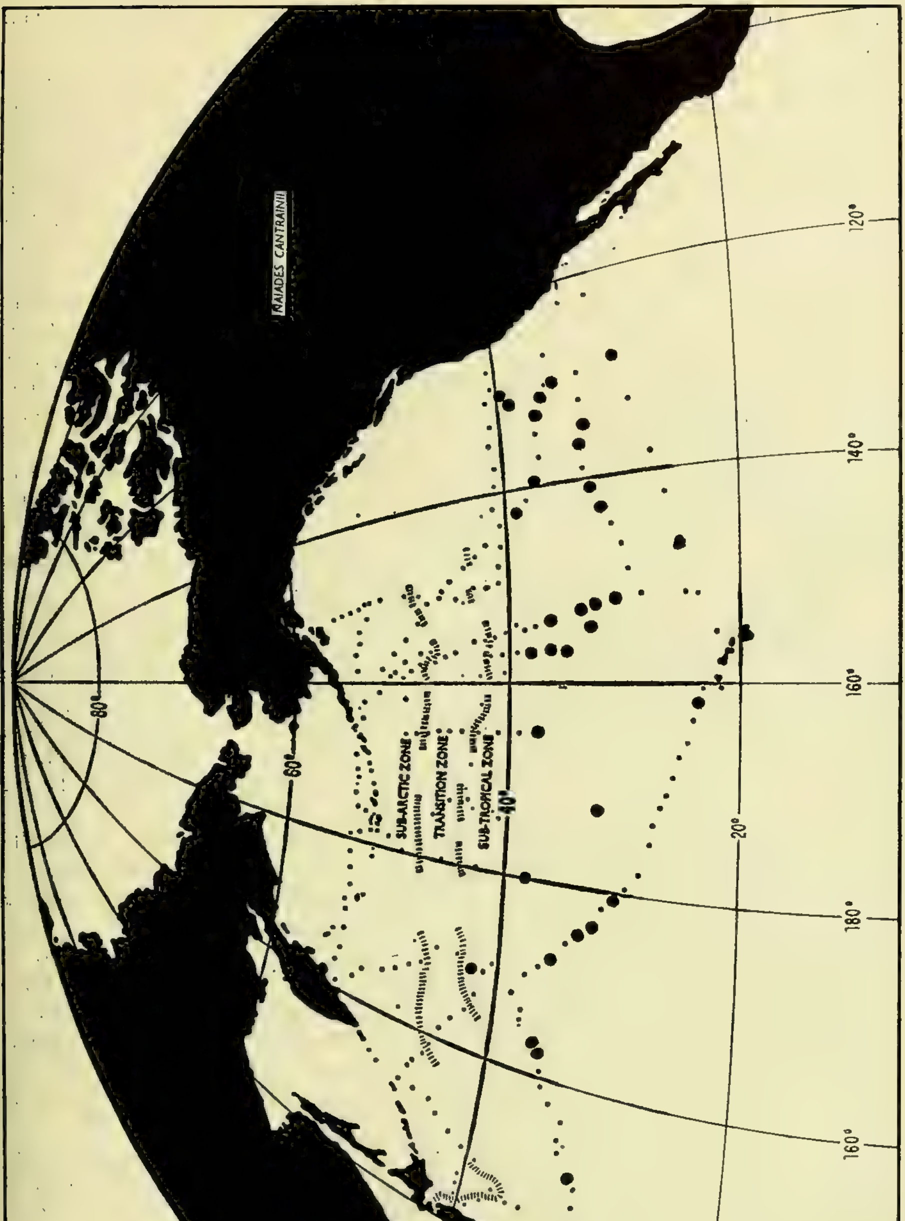
NAIADES CANTRAINII
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 36. Occurrence of *Naiades cantrainii.*

material came from the surface water off Hawaii, and Dales (1957) recorded it from the top 75 m. of water in the California Current.

Except for one record from Trans-Pacific Expedition Stn. 51A in the Transition Zone, all the records of *V. longissima* are from the Sub-Tropical Zone, where it occurred at numerous stations across the breadth of the North Pacific (Text-fig. 38). The largest number of specimens in any sample was eight at Trans-Pacific Expedition Stn. 104A, equivalent to twenty-one per 1,000 m³ of water. Only one specimen was collected at Stn. 51A, and statistically such a record could be discarded, and the northerly limit to the distribution of *V. longissima* taken to be the northern boundary of the Sub-Tropical Zone, but in fact this one apparently anomalous record may cloak a potentially significant biological relationship. Thus, in the Systematic Account (above p. 393), it is noted that this one specimen had dark brown spots on the head and that specimens from other stations in the Sub-Tropical Zone, but close to the boundary with the Transition Zone, also exhibit this hitherto unreported character. It is possible therefore that a separate population of *V. longissima* inhabits the Transition Zone and immediately adjacent water to the south.

All records of *V. longissima* are from the nets towed open to the surface, and it may therefore be considered an inhabitant of the upper layers of the North Pacific Central water. It has previously been reported from the Sub-Tropical Zone of the North Pacific by Izuka (1914 as *V. grandis*), Treadwell (1943, as *Torrea fasciata*), Uschakov (1957*a*, as *V. pacifica*) and Dales (1957).

V. crystallina was collected only in the Sub-Tropical Zone, appearing at numerous stations (Text-fig. 39), and the southern boundary of the Transition Zone may be taken as the northern limit of its distribution in the North Pacific. It must penetrate into deep water there only rarely for all nets collecting it fished in the upper 400 m. The largest number collected was three, at Trans-Pacific Expedition Stn. 85A, equivalent to six per 1,000 m³ of water. Dales (1957) reported *V. crystallina* from the California Current, this being the first record of the species from the North Pacific.

V. formosa did not occur at many stations, but these were scattered across the Sub-Tropical Zone (Text-fig. 40) and it is clear that it does not penetrate north of this region. Collected exclusively by nets towed open to the surface *V. formosa* must at the present state of our knowledge be considered a surface water species. Only rarely was there more than one specimen in a sample. The first record of *V. formosa* from the North Pacific was made by Treadwell (1943) from the Sub-Tropical Zone ; later Dales (1957) found it at sixty-seven stations in the California Current, in marked contrast to the comparatively few records made here. Because more than half of the latter are from east of 140° W., it may be that it is in this area of the North Pacific that the main concentrations of this species are to be found.

Known exclusively from the North Pacific Ocean *V. tagensis* was present in only seventeen of the 416 samples examined. Twelve of these are from nets closed at depth (between 680–130 m.) and the remainder from nets towed through a considerable distance open to the surface so that the species can be considered a deeper water form. The few records made may be explained by the smaller number of

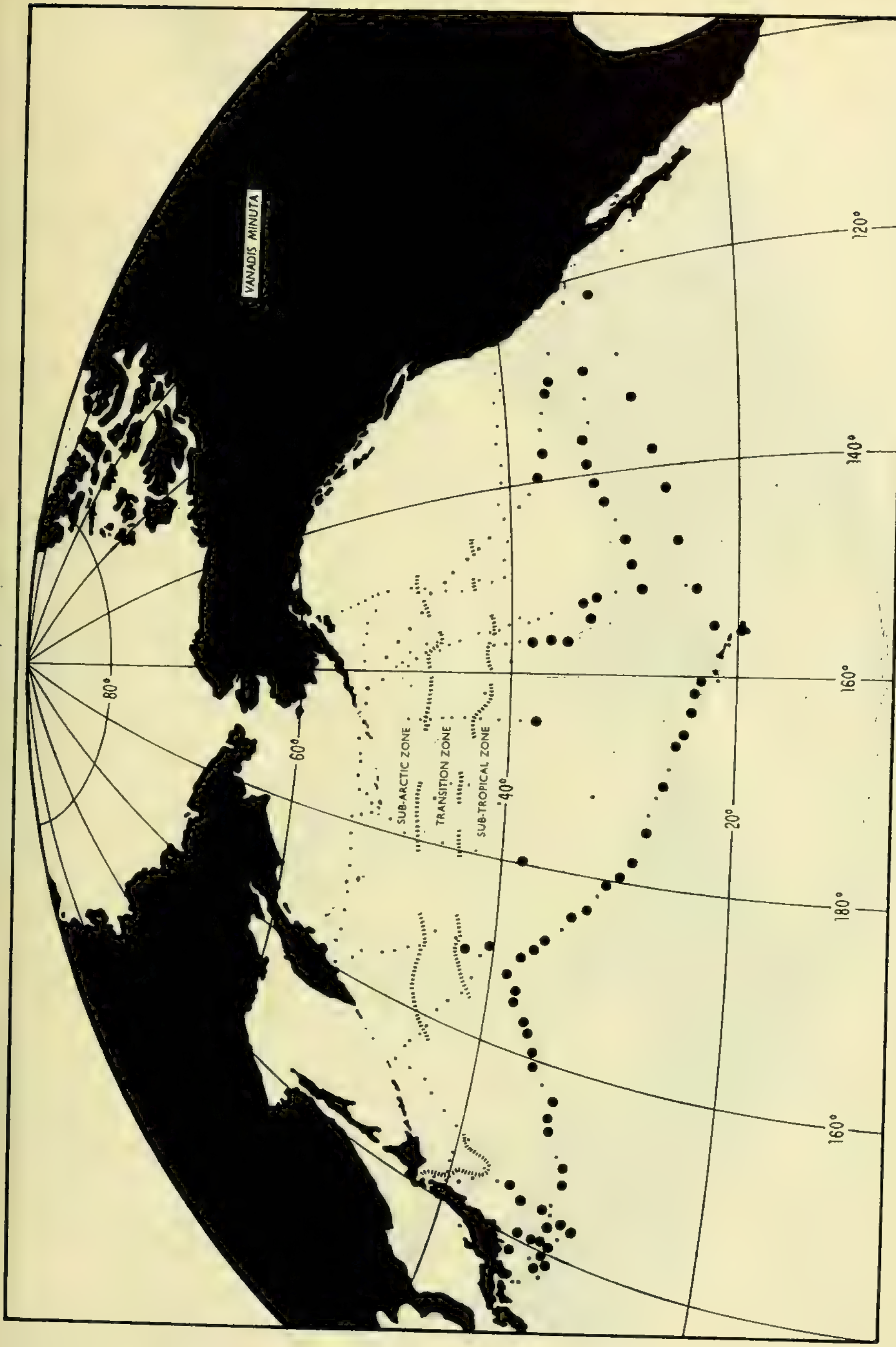
VANADIS MINUTA
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 37. Occurrence of *Vanadis minuta.*

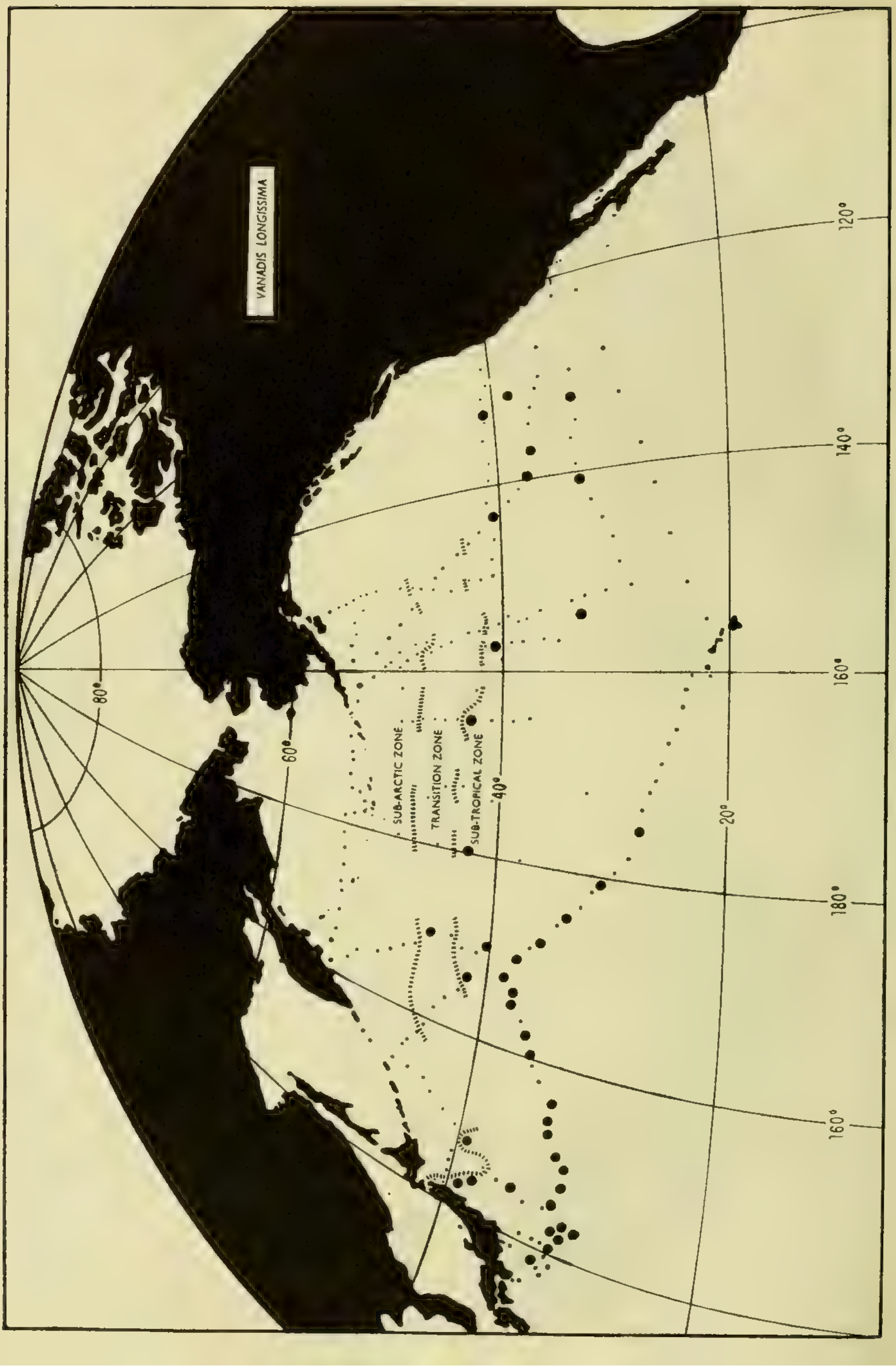
VANADIS LONGISSIMA
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

Fig. 38. Occurrence of *Vanadis longissima*.

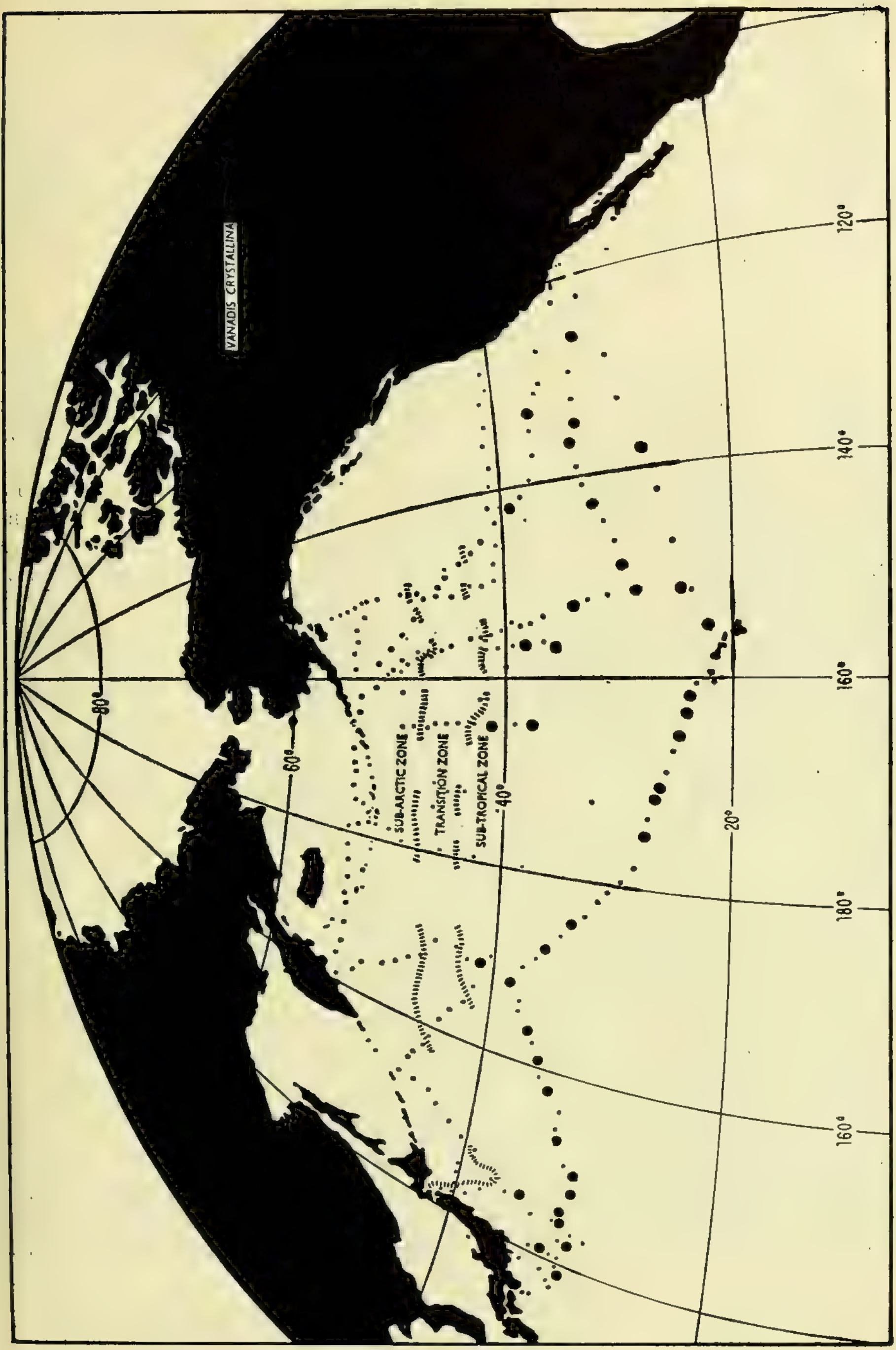
VANADIS CRYSTALLINA
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 39. Occurrence of *Vanadis crystallina*.

nets which were closed at depth (Table I). None of the catches of *V. tagensis* was north of the Sub-Tropical Zone (Text-fig. 40) and it is possible that the northern boundary of this region restricts its movement into the higher latitudes. At two stations two specimens were caught but at the others only one was collected. The original records of *V. tagensis* were made from Monterey Bay, between 500–1,000 m. (Dales, 1955) and it is apparent that the late discovery of this species, and the comparatively limited area from which it is known, is due to its deep water habitat, for few expeditions can sample the deep layers as exhaustively as they do the surface waters. A much wider range of distribution for this species may become apparent when more deep water collections have been made.

RHYNCHONERELLA

Four species of this genus were present in the collections. *R. petersii* and *R. mobii* in the Sub-Tropical and Transition Zones, *R. gracilis* mainly in these two but also at a few stations in the Sub-Arctic and *R. angelini* in some abundance in all three.

R. petersii was found at numerous stations in the Sub-Tropical Zone and occasionally penetrates into the Transition Zone (Text-fig. 41), the northern boundary of the latter region probably restricting its movement into higher latitudes. At most stations only one specimen was collected but four were in the sample from Stn. 11A of the Trans-Pacific Expedition. This is equivalent to five per 1,000 m^3 of water. Clearly the species must only rarely occur in abundance. Most records are from the top 300 m. of water, but at Stn. 12F a net towed between 850–680 m. collected one specimen. This record must be treated as an anomaly until extensive collections at depth prove otherwise. The only previous record of *R. petersii* from the North Pacific was made by Uschakov (1957*a*, as *Callizona setosa*) from the Sub-Tropical Zone in the Western Pacific. *R. petersii* is not well known from other oceans in the world but has not been reported outside Tropical and Sub-Tropical waters.

R. mobii was found at comparatively few stations. These, however, were all within the Sub-Tropical Zone (Text-fig. 42) indicating that it rarely moves further north than this region. There was never more than one specimen of this species in a sample. It was collected in nets towed open in the top 400 m. of water and in closing nets hauled between 370–140 m. Evidently *R. mobii* is principally an inhabitant of the upper waters; Dales (1957) first recorded it in the North Pacific from the surface waters of the California Current. Elsewhere in the world *R. mobii* is known from few records but these are all from Tropical and Sub-Tropical waters.

R. gracilis was present in numerous samples most of which came from the Sub-Tropical Zone (Text-fig. 43). It also appeared, however, in the Transition Zone and at two stations in the Sub-Arctic Zone. If, as is probable, *R. gracilis* has its northern limit of distribution at the southern boundary of the Sub-Arctic Zone the specimens collected beyond this boundary could be explained as accidental survivors outside their hydrological limits. This may be true of the specimen from Trans-Pacific Expedition Stn. 48D but is almost certainly not applicable to that

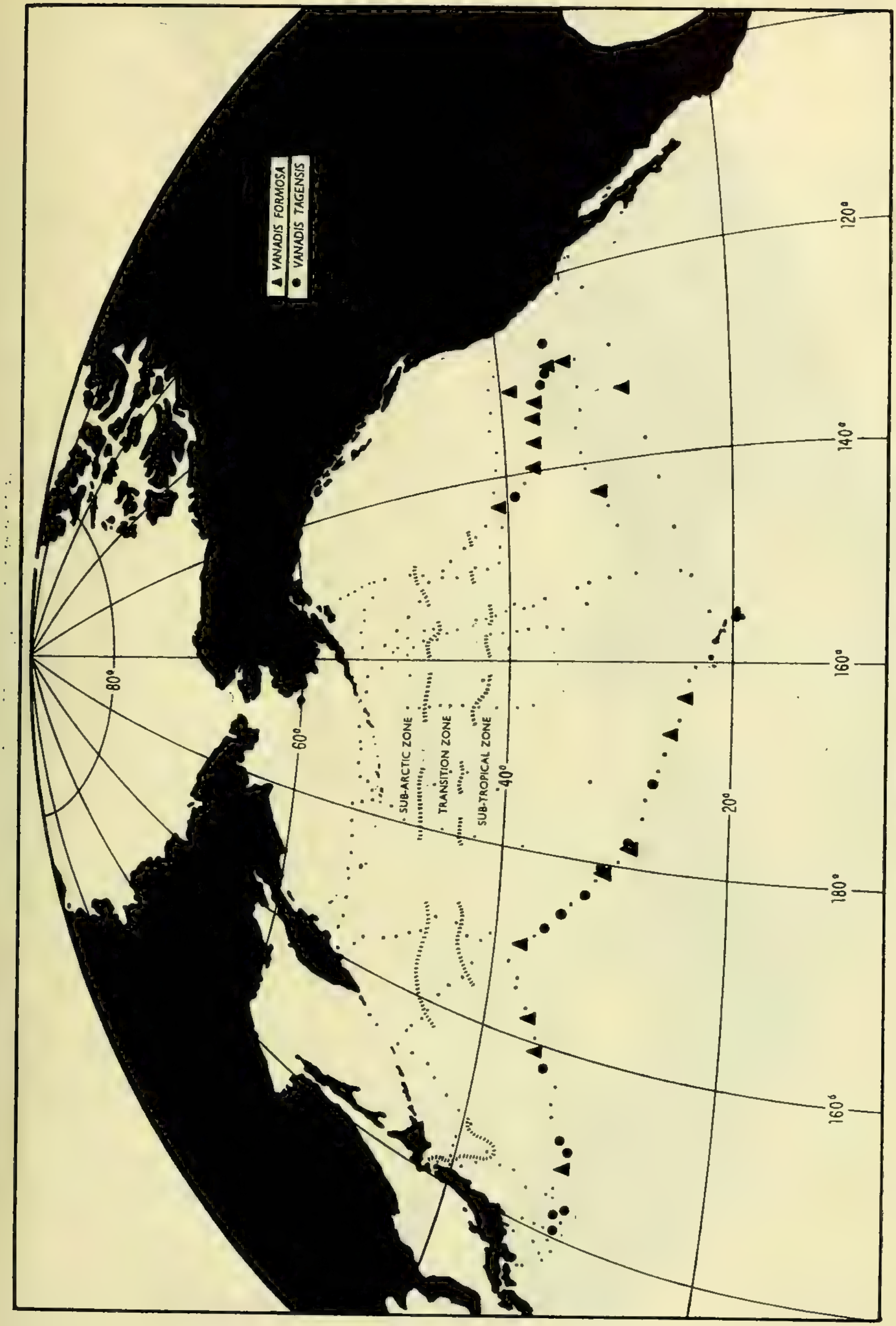
▲ VANADIS FORMOSA
● VANADIS TAGENSIS
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 40. Occurrence of *Vanadis formosa* and *V. tagensis*.

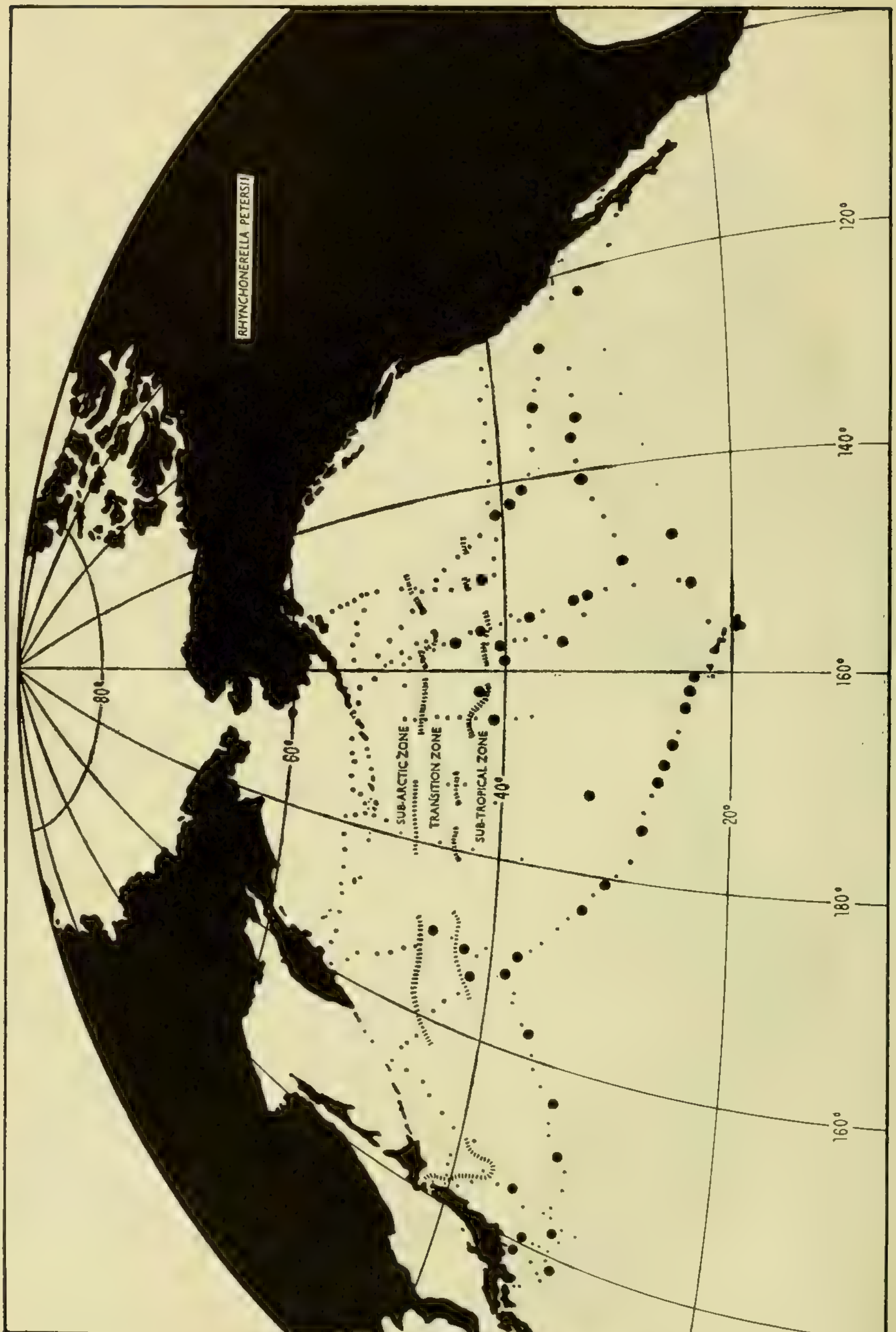
RHYNCHONERELLA PETERSII
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 41. Occurrence of *Rhynchonerella petersii.*

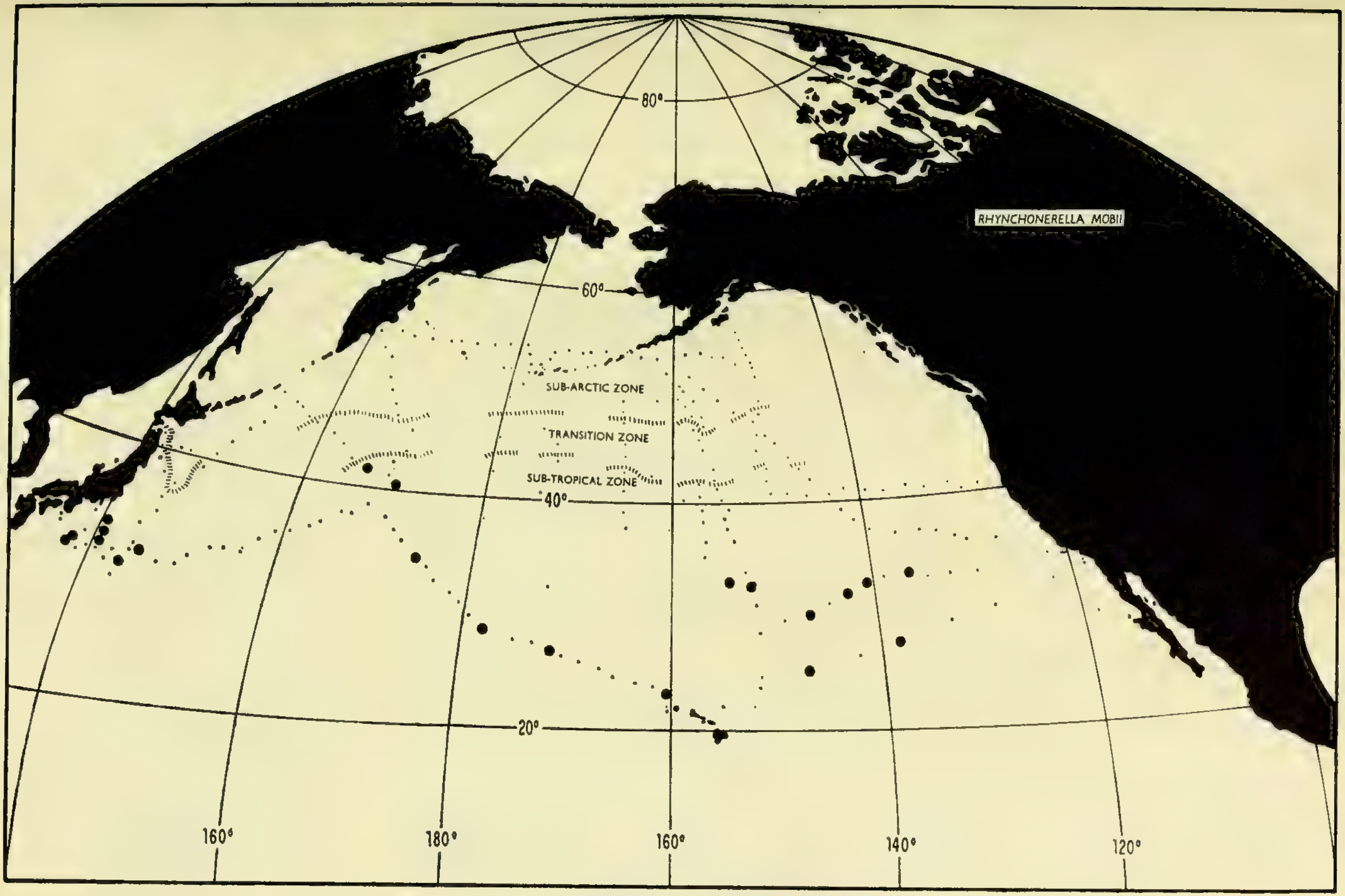
RHYNCHONERELLA MOBII
80°
60°
40°
20°
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
160°
180°
160°
140°
120°

FIG. 42. Occurrence of *Rhynchonerella mobii.*

from Northern Holiday Exp., Stn. 26, which is much further north of the boundary line, and within the region of the Alaskan gyral. Further collections from the North East Pacific will have to be examined before it can be established that *R. gracilis* does not inhabit this region as an occasional, possibly seasonal migrant.

R. gracilis was collected mainly by nets which were towed open to the surface; the majority of these fished only in the top 400 m. of water within which layer the species appears to concentrate. In most samples only one specimen was collected but six were caught at Stn. 110A, of the Trans-Pacific Expedition equivalent to twelve per 1,000 m^3 of water.

R. gracilis was first reported from the North Pacific, off Misaki, Japan, by Izuka (1914 as *Callizona japonica*) and subsequently by Uschakov (1957*a* as *C. nasuta*) from between 35–40° N., about 151° E., and Berkeley & Berkeley (1960) with one record as far north as 54° 30′ N., about 152° W., and two others in the Transition Zone.

R. angelini was found in all three hydrological zones (Text-fig. 44). This was to be expected if its pattern of distribution in the Atlantic Ocean, as suggested by Tebble (1960), was to be repeated in the Pacific. Thus, although restricted in its movements southwards, in the southern hemisphere by the Sub-Tropical Convergence, there is no comparable restriction in the northern hemisphere. In the latter there are no endemic pelagic polychaetes in higher latitudes and some of the species there may be taken to represent Antarctic endemic elements in boreal waters, *R. angelini* for instance representing the endemic antarctic *R. bongraini*; the evidence found in the present work suggests that this is now applicable to the North Pacific in the case of these species of *Rhynchonerella*.

Throughout all three hydrological zones *R. angelini* was caught in nets towed open in the top 200–300 m. of water and in some nets closing between 500 and 121 m. Only on very few occasions were more than one specimen collected.

R. angelini was first recorded from the North Pacific by Moore (1908 as *Callizona angelini*) in the stomachs of salmon caught off the coast of Alaska, and was subsequently reported under the same name by Berkeley (1930), from the east coast of Vancouver, by Berkeley & Berkeley (1957, 1958 and 1960), from the Sub-Arctic Zone, and the Sub-Tropical Zone; Treadwell (1943 as *Rhynchonerella pycnocera*) reported it from the Sub-Tropical Zone and Dales (1955 and 1957) from Monterey Bay and the California Current.

PLOTOHELMIS

P. tenuis was found at numerous stations across the Sub-Tropical Zone and in a few samples in the Transition and Sub-Arctic Zones (Text-fig. 45). Most of the records from the latter region were near its southern boundary and probably indicate minor intrusions of warmer water. Nevertheless, in suggesting that the southern boundary of the Sub-Arctic Zone restricts the northerly movement of *P. tenuis* in the North Pacific, I draw attention to these records, for they may indicate a seasonal migration outside the normal hydrological limits of the species. *P. tenuis* was found in open and closing nets at all depths from 850 m. to the surface, occurring

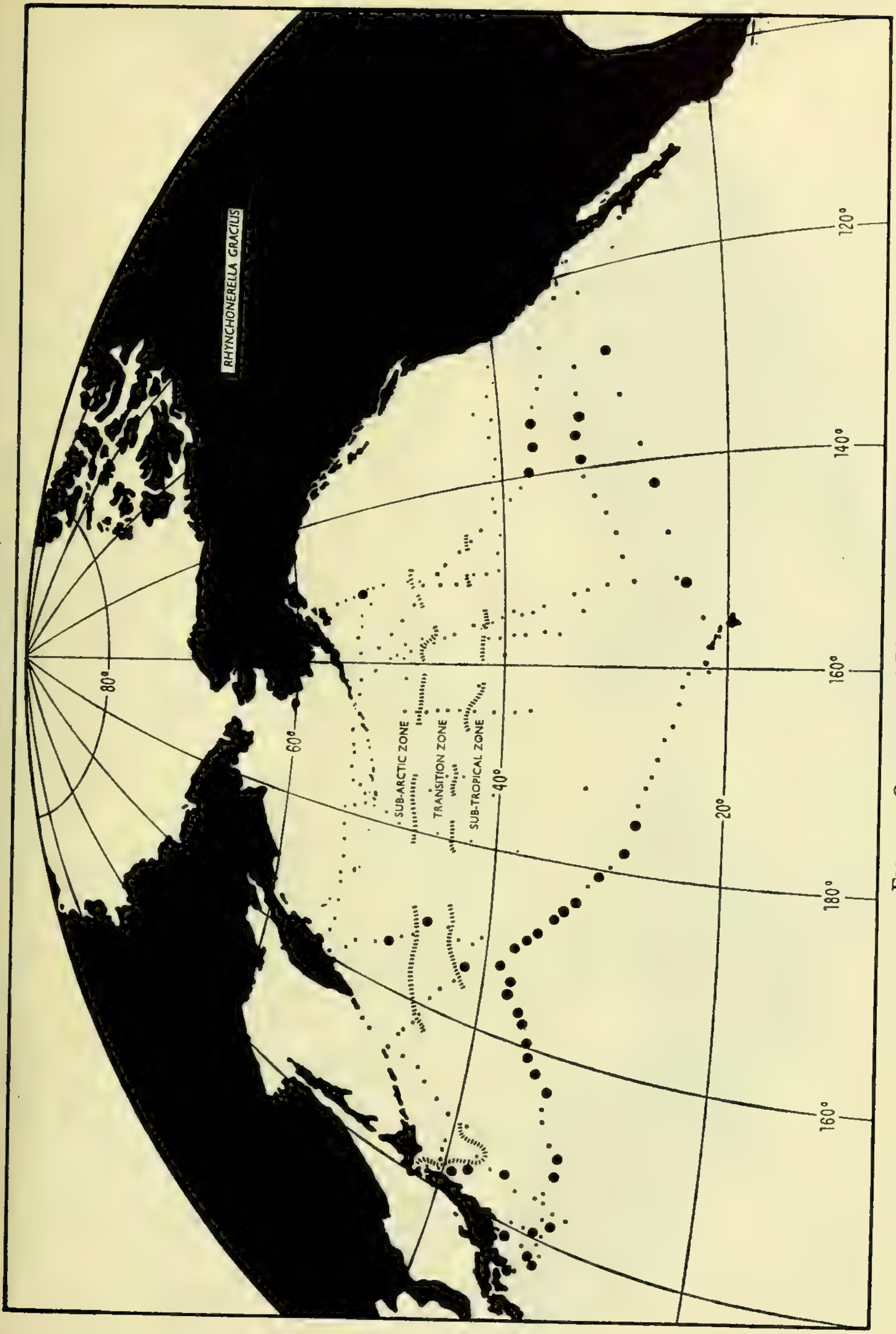
RHYNCHONERELLA GRACILIS
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 43. Occurrence of *Rhynchonerella gracilis*.

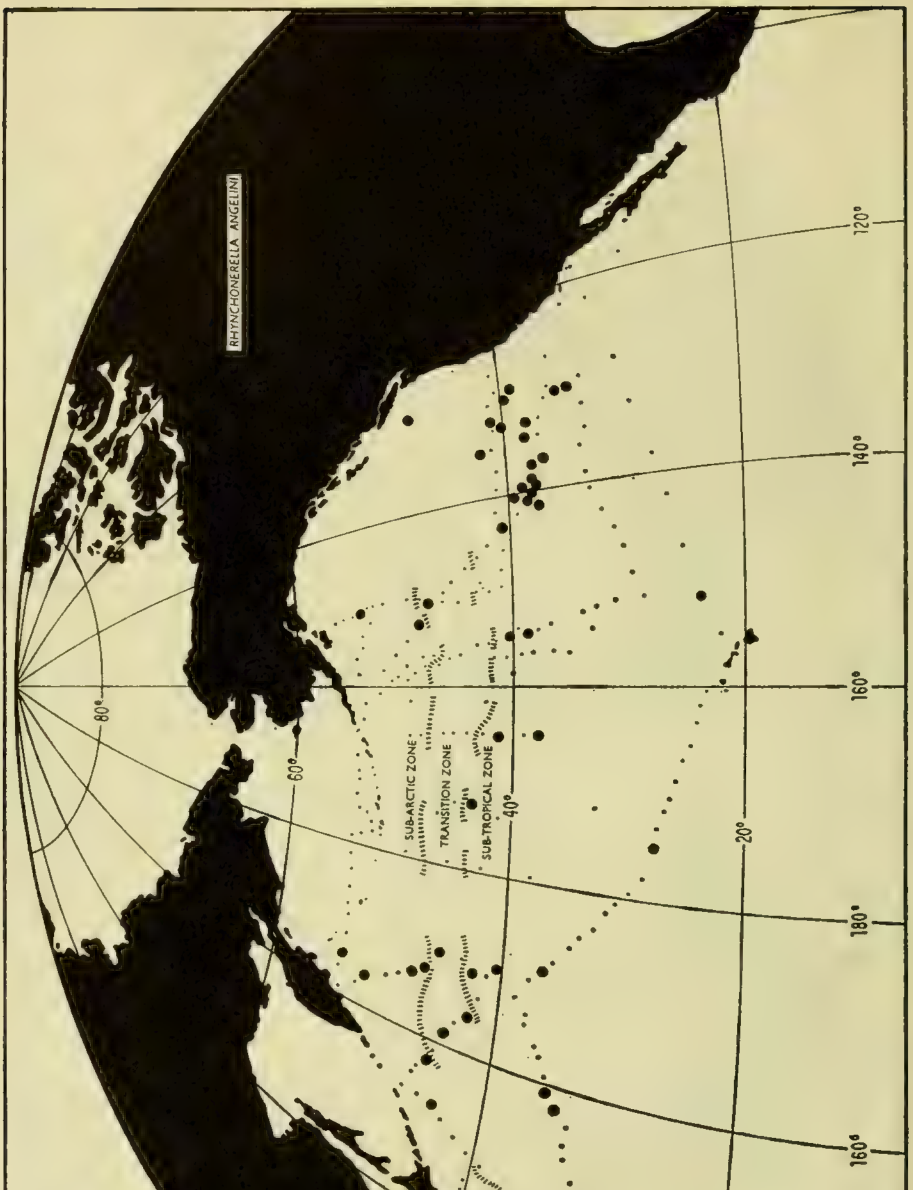
RHYNCHONERELLA ANGELINI
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 44. Occurrence of *Rhynchonerella angelini.*

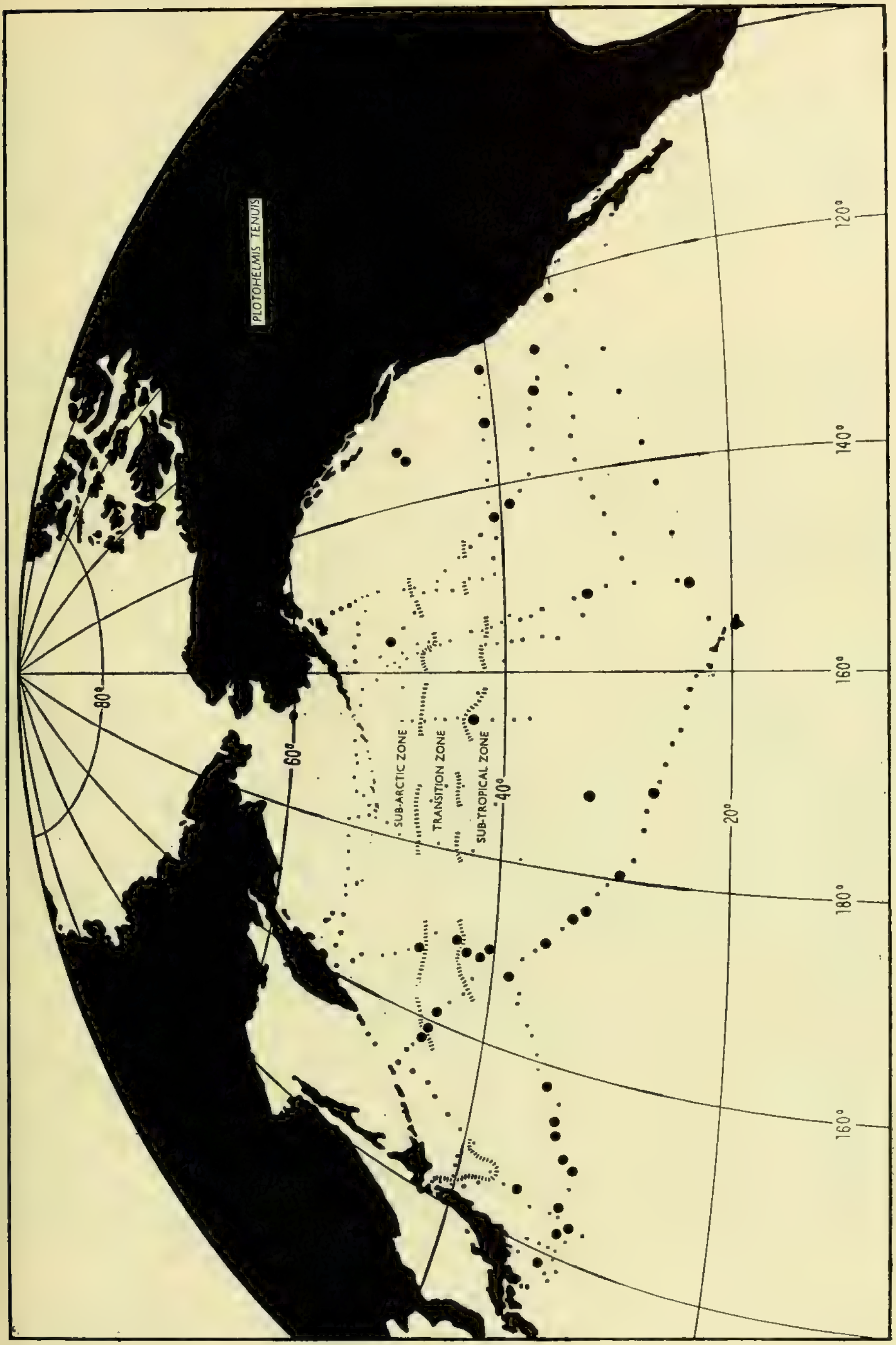
PLOTOHELMIS TENUIS
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 45. Occurrence of *Plotohelmis tenuis*.

more frequently in the upper layers where most nets fished. Only on few occasions were more than one specimen collected but an exceptionally large catch was made at Northern Holiday Station 2, sixty-nine specimens, equivalent to 110 per 1,000 m^3 of water, being caught. Izuka (1914) was the first to describe this species from the North Pacific as *Rhynchonerella fulgens* from off Misaki, Japan, and Dales reported it from Monterey Bay (1955) and in the California Current (1957). Elsewhere in the world *P. tenuis* is known from comparatively few records and the limits to its distribution cannot be precisely fixed, but it is probably a Sub-Tropical and Tropical species.

KROHNIA

Krohnia lepidota was found only in the Sub-Tropical Zone (Text-fig. 46) and it is doubtful if it ever occurs further north than this region. It was collected entirely by nets fishing in the top 370 m. of water and at most stations only one specimen was found, but four were present at Trans-Pacific Expedition Stn. 97A, equivalent to five per 1,000 m^3 of water.

Chamberlin (1919) first recorded *K. lepidota* from the North Pacific as *Rhynchonerella cincinnata* off the SW. coast of Mexico and Treadwell (1943) reported it as *Callizona pigmenta* from 12° 40′ N., 137° 32′ W. Elsewhere in the world *K. lepidota* is known only from Sub-Tropical and Tropical waters.

TYPHLOSCOLECIDAE

Six species of this family were present in the collections. Of these the cosmopolitan *Typhloscolex mülleri* was very common everywhere, and *Sagitella kowalewskii* and *Travisiopsis lobifera* were present in abundance in the Sub-Tropical Zone; however, the other three species *Travisiopsis levenseni*, *lanceolata* and *dubia* were collected only rarely and it is not possible to be conclusive about their distributional limits.

Typhloscolex mülleri was found in all three hydrological zones occurring in greatest abundance in the Sub-Arctic (Text-fig. 47). It was collected at all explored depths, in both open and closing nets. These records confirm the known distribution of this species in the North Pacific where it has been reported from the Sub-Tropical and Sub-Arctic by Treadwell (1943) and Uschakov (1957*a*); the Sub-Arctic by Uschakov (1952, 1955) and Berkeley & Berkeley (1948, 1957, and 1960); the Transition Zone by Berkeley & Berkeley (1960) and the California Current by Dales (1957). In addition Uschakov (1957*b*) records it from high Arctic waters in approximately 80° N., near 180°. It has been noted in the Systematic Account (pp. 408–409) that in the North Pacific an ecotype of *T. mülleri* inhabits the Sub-Arctic Zone.

Sagitella kowalewskii was present at a large number of the stations made in the Sub-Tropical Zone; indeed the persistence of its occurrence there was a feature of the collections (Text-fig. 48). It is probable therefore that the southern boundary of the Sub-Arctic Zone marks the northern limit of its distribution although one specimen was found just north of this boundary. Generally no more than ten

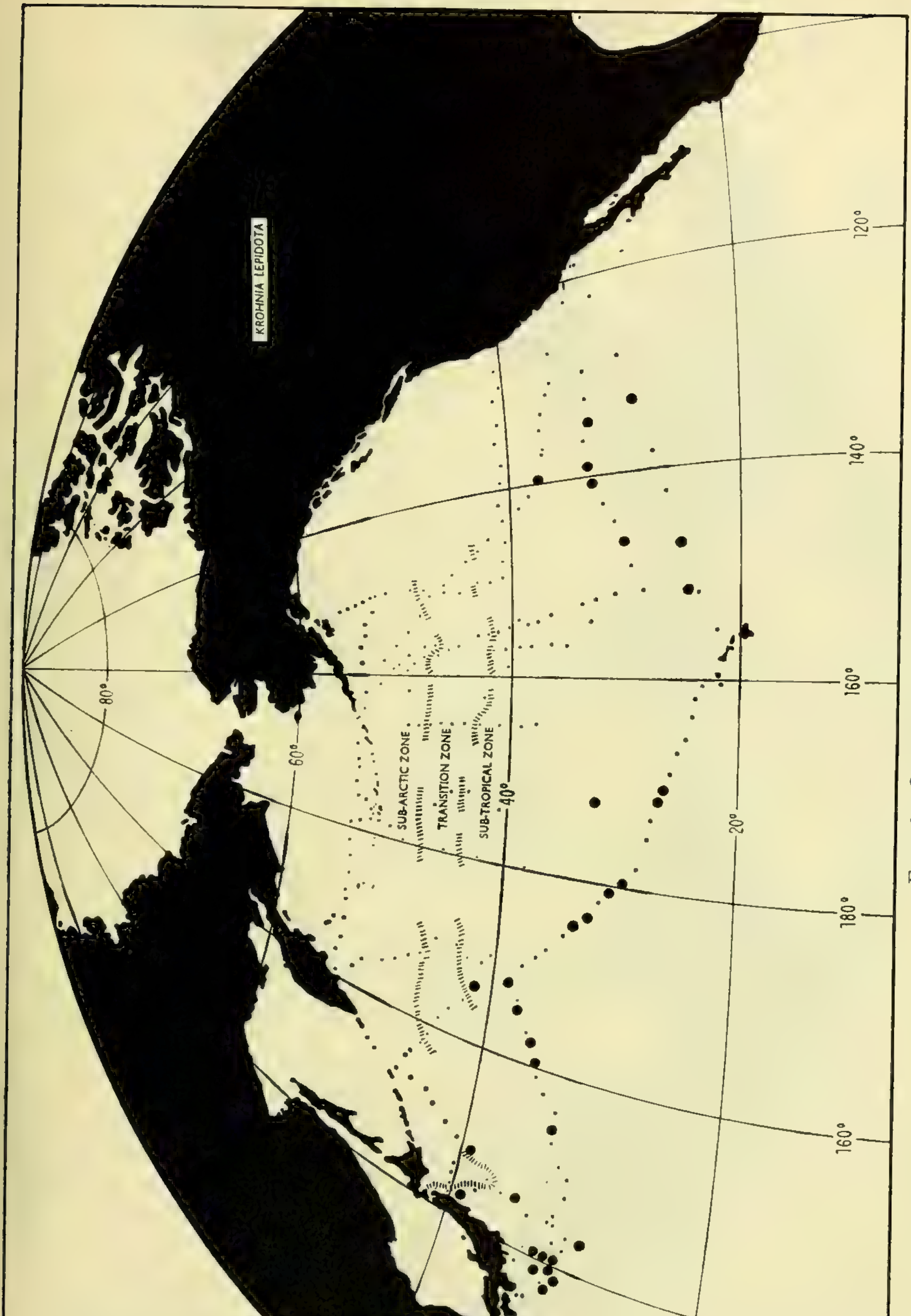
KROHNIA LEPIDOTA
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

Fig. 46. Occurrence of *Krohnia lepidota*.

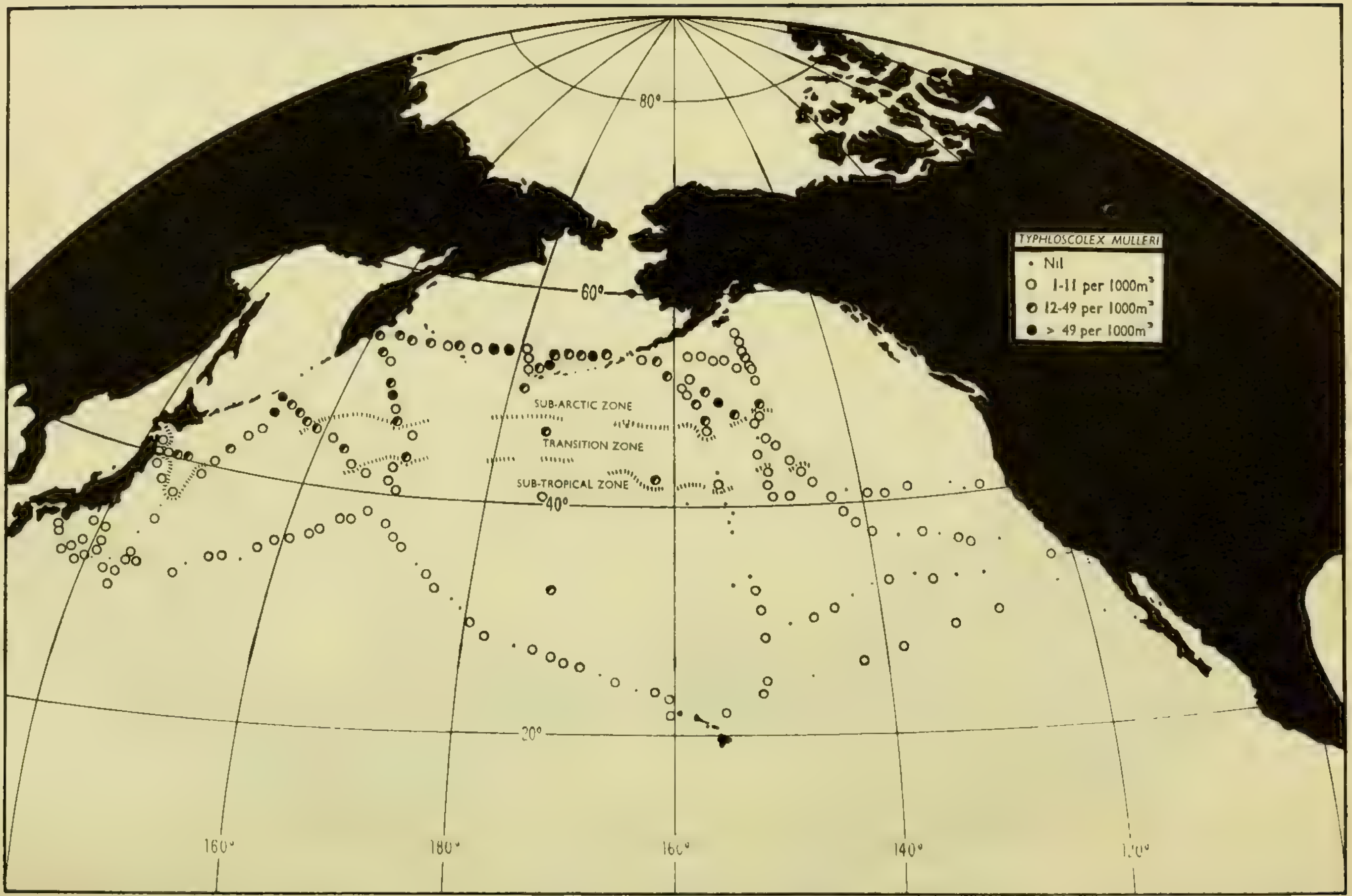
TYPHLOSCOLEX MULLERI
• Nil
○ 1-11 per 1000m³
● 12-49 per 1000m³
● > 49 per 1000m³
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
160°
180°
160°
140°
120°

FIG. 47. Occurrence of *Typhloscolex mulleri*.

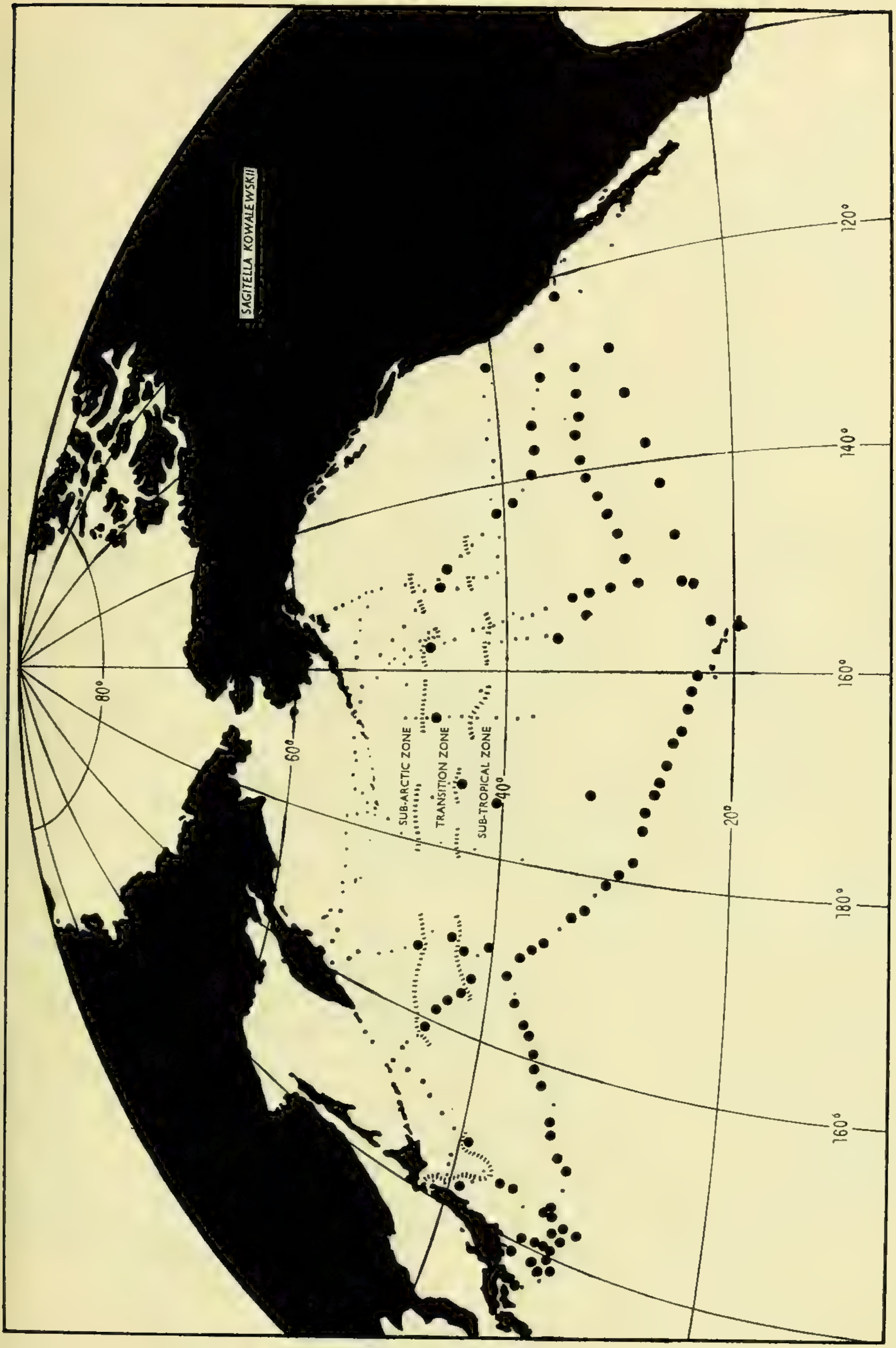
SAGITELLA KOWALEWSKII
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

Fig. 48. Occurrence of *Sagitella kowalewskii*.

specimens of *S. kowalewskii* were present in a sample with exceptionally fourteen at Stn. 86A of the Trans-Pacific Expedition, equivalent to thirty per 1,000 m^3 of water filtered. It was found at all explored depths in both open and closing nets, and evidently is capable of a wide distribution in deep and surface water circulations.

Berkeley (1930) was the first to record *S. kowalewskii* from the North Pacific, finding it off Vancouver Island ; subsequently Okuda (1937, 1938) reported it from sub-tropical water off Japan and Treadwell (1943 as *Plotobia paucichaeta*) and Uschakov (1957*a*) recorded it from the Sub-Tropical and Transition Zones, and Dales (1957) found it in the California Current ; Uschakov (1957*a*), however, also records it off Kamchatka in about 52° N., well within the Sub-Arctic Zone. I hesitate to accept this record in the face of no supporting evidence from other expeditions, notwithstanding Berkeley & Berkeley's (1960) record from 50° N., in the north-east Pacific which I consider an area to which the species could migrate within the Alaskan gyral (Text-fig. 2).

Travisiopsis lobifera was collected at numerous stations across the Sub-Tropical Zone and appeared also in the Transition Zone where the northern boundary probably restricts its movement northwards (Text-fig. 49). On few occasions were more then ten specimens collected but an exceptional catch was made at Trans-Pacific Expedition Stn. 99A, where fifty-four specimens were caught, equivalent to forty-two per 1,000 m^3 of water. Most nets collecting this species fished in the upper 330 metres but it was also caught between 680 and 130 metres suggesting that it inhabits a considerable depth of water. Although persistent in its occurrence in the western and eastern North Pacific *T. lobifera* was only rarely found south of 40° N., between 140° W., and 180°.

The first record of *T. lobifera* from the North Pacific was made by Dales (1955) from Monterey Bay, who in 1957 also reported it from the California Current. Uschakov (1957*a*) reported it from the northern region of the Transition Zone in the western North Pacific and Berkeley & Berkeley (1957 and 1960) from the same zone in the eastern North Pacific. This last record includes one from 51° 21′ N., 149° 21′ W., the farthest north the species has ever been recorded, and with that made by Uschakov (1957*a*) is additional evidence for the suggestions made above that it is the northern boundary of the Transition Zone that marks the northern limit of its distribution.

Travisiopsis levinseni is known from the North Pacific only through the records made by Dales (1955) from deep water in Monterey Bay and the three made here from the Trans-Pacific Expedition (Text-fig. 50). The latter are from nets which could have collected it in deep water but clearly little can be said about its distribution until more records are available. The few records made may be due to lack of extensive sampling of the deeper layers. In the Atlantic Ocean *T. levinseni* is known from all extremes of hydrological conditions (Støp-Bowitz, 1948 ; Tebble, 1960) and is generally considered a cosmopolitan species.

Travisiopsis lanceolata was collected at only nine stations, these being mainly in the Sub-Tropical Zone but two catches were made in the Transition Zone and one in the Sub-Arctic (Text-fig. 50). Most of these were by nets closing at depth but more extensive collecting in the deeper water will be required in order to define the

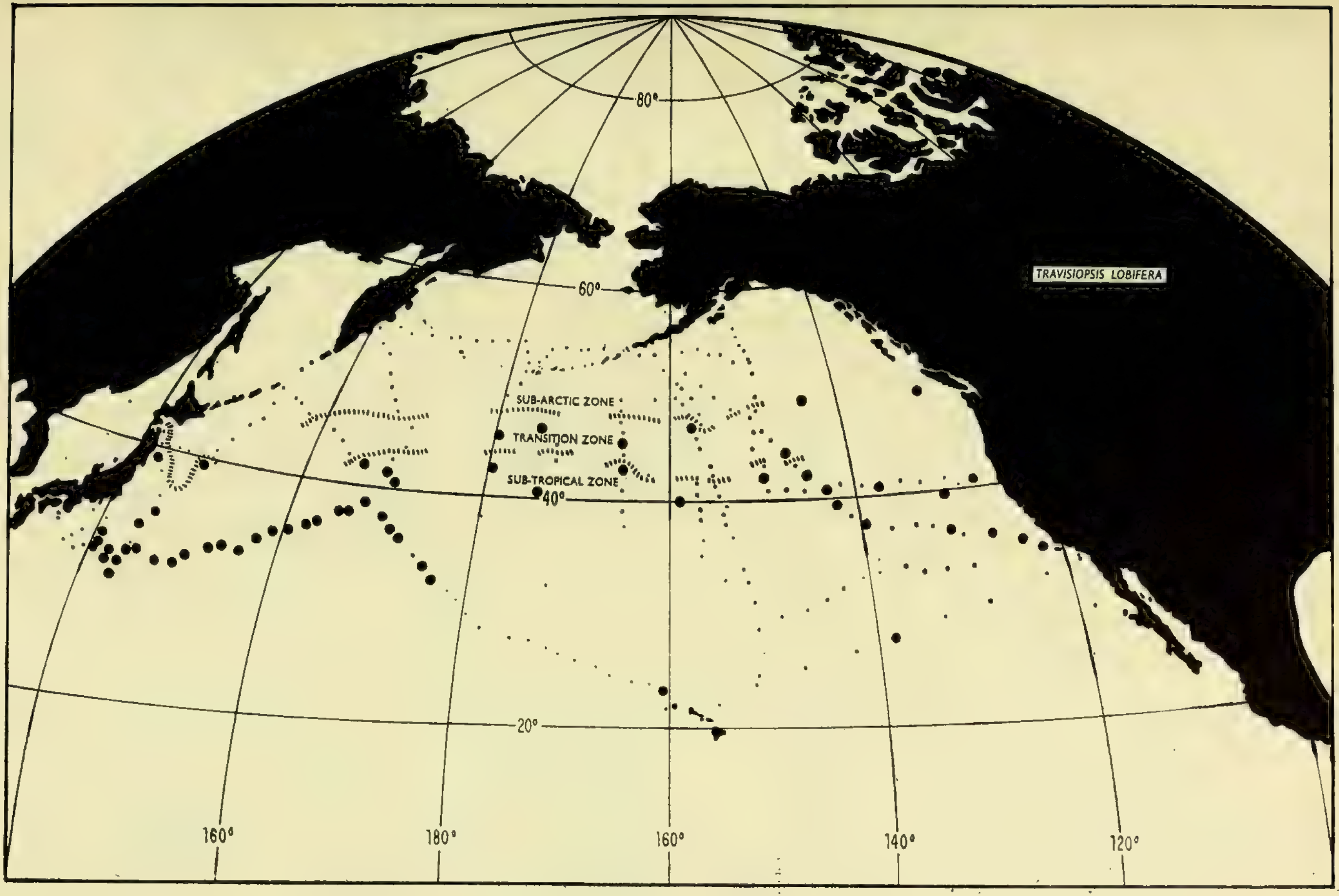
TRAVISIOPSIS LOBIFERA
80°
60°
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
40°
20°
160°
180°
160°
140°
120°

FIG. 49. Occurrence of *Travisiopsis lobifera.*

limits of its distribution. *T. lanceolata* was first recorded from the North Pacific by Treadwell (1943 as *Plotobia simplex*), from five records in the Sub-Arctic Zone and two in the Sub-Tropical. All these records suggest that this species inhabits both warm and cold water regions of the North Pacific as it does in the North Atlantic (Støp-Bowitz, 1948).

Travisiopsis dubia was collected at only eight stations, all in the Sub-Tropical Zone (Text-fig. 50) and all in nets towed open to the surface. These are the first records of this species from the North Pacific and only Dales (1960) has previously reported it from the South Pacific. Dales' records were made possible through the collections of the Trans-Pacific Expedition, which I was able to show him were identical with material he had from the South China Sea. Otherwise known only through its original discovery in the Atlantic Ocean by Støp-Bowitz (1948) from 39° 30′ N., 49° 42′ W., and 48° 24′ N., 36° 53′ W., *T. dubia* is not known from sufficient records for its distribution to be comprehensively analysed. Moreover, because it is very like *Sagitella kowalewskii* (see above, p. 415), it may have been overlooked among previous collections of this species and these will have to be re-examined before the situation is clarified.

PHYLLODOCIDAE (LOPADORHYNCHINAE AND IOSPILINAE)

Eight species of this family are reported here, showing a diversity of generic and specific distribution not met with in any other family of pelagic polychaetes.

LOPADORHYNCHINAE

PELAGOBIA

Pelagobia longicirrata was collected in all three hydrological zones (Text-fig. 51). This was as expected for in the Atlantic it has been reported from all extremes of hydrological conditions (Støp-Bowitz, 1948 ; Tebble, 1960) and is generally accepted as a cosmopolitan species. It occurred in its greatest abundance in the Sub-Arctic Zone with sixty-five specimens at Stn. 40C of the Trans-Pacific Expedition, equivalent to one hundred and ninety-five per 1,000 m^3 of water. This was the largest catch made at any station. There were numerous stations in this zone however where no more than one to five specimens of *P. longicirrata* were collected per 1,000 m^3, as was common in the Sub-Tropical Zone. In all hydrological zones it appeared at all explored depths but had its greatest abundance in the nets closed between 700 and 300 metres. Clearly this species has a very wide depth range in the North Pacific, similar to that found in the Sub-Antarctic and Antarctic Zones of the South Atlantic by Tebble (1960).

The first record of *P. longicirrata* from the North Pacific was made by Chamberlin (1919, as *P. vigueri*) from the Tropical Zone, subsequently Okuda (1937, 1938), Treadwell (1943, as *P. vigueri*), Dales (1955, 1957), Uschakov (1957*b*), and Berkeley & Berkeley (1960) reported it from the Sub-Tropical Zone and Treadwell (1943), Uschakov (1952 as *P. vigueri* ; 1957*a*) and Berkeley & Berkeley (1960) found it in the Transition and Sub-Arctic Zones. It was also reported from north of 76° N., by Uschakov (1957*b*), the most northerly record for the species.

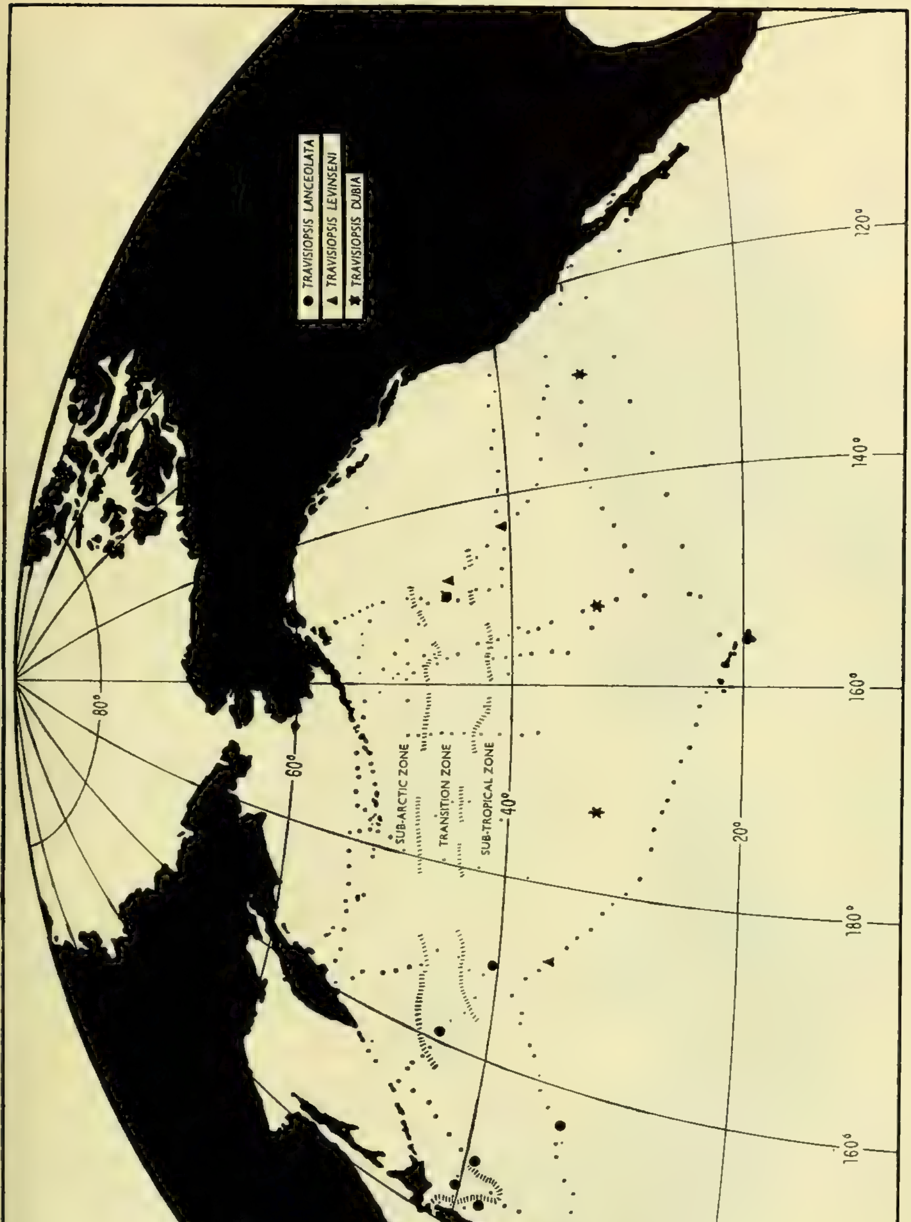
● TRAVISIOPSIS LANCEOLATA
▲ TRAVISIOPSIS LEVINSENI
★ TRAVISIOPSIS DUBIA
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 50. Occurrence of *Travisiopsis lanceolata*, *T. levinseni* and *T. dubia*.

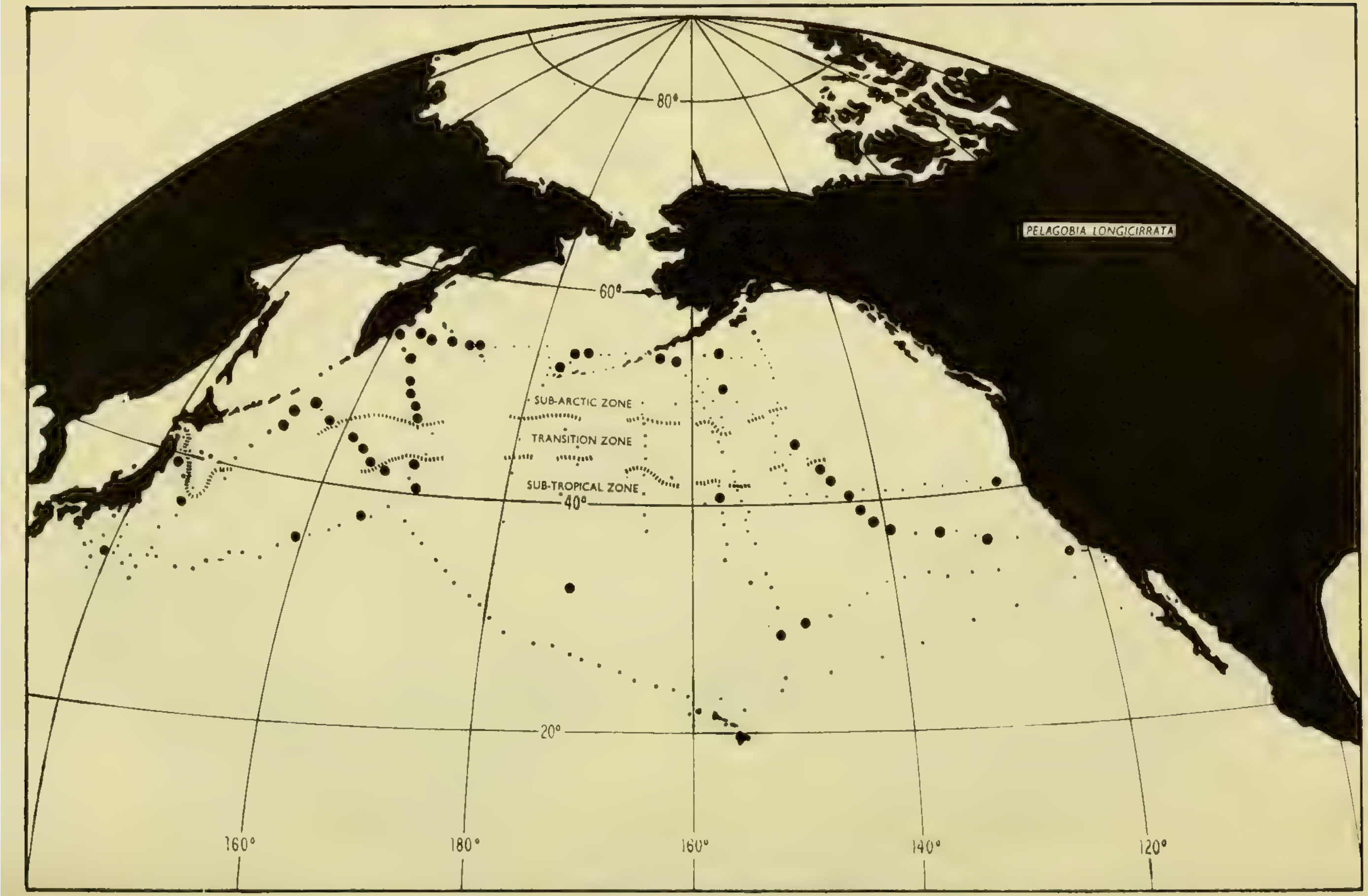
80°
PELAGOBIA LONGICIRRATA
60°
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
40°
20°
160°
180°
160°
140°
120°

FIG. 51. Occurrence of *Pelagobia longicirrata*.

LOPADORHYNCHUS

Three species of this genus are reported here, *L. krohnii*, *L. uncinatus* and *L. brevis*. All three were collected only within the Sub-Tropical Zone, and elsewhere in the world are known only from Tropical and Sub-Tropical waters.

Lopadorhynchus krohnii was present at numerous stations (Text-fig. 52) and clearly never penetrates north of the Sub-Tropical Zone. It was rare for more then one or two specimens of this species to be in any sample but six were caught at Stn. 61 of the Northern Holiday Expedition, equivalent to eight per 1,000 m^3 of water. It was collected exclusively in nets towed in the upper 370 metres, and must be essentially a surface water species. This appears to be only the second record of *L. krohnii* from the North Pacific, Dales (1957) having first recorded it from the California Current.

L. uncinatus was collected at only eleven stations (Text-fig. 53) but these ranged across the ocean and were also close to the northern boundary of the Sub-Tropical Zone which almost certainly restricts its movement northwards. Although not caught very often, on only one occasion was more than one specimen collected, *L. uncinatus* was present in nets towed a little deeper than those which caught *L. krohnii*, and it may inhabit a greater depth range. *L. uncinatus* was first recorded from the North Pacific by Treadwell (1943 as *L. varius*) at seven stations made by the *Carnegie* in the Tropical and Sub-Tropical Zones between San Francisco and the Marshall Is.: Dales (1955 and 1957) subsequently reported it from Monterey Bay and the California Current and Berkeley & Berkeley (1958) found it at 20° 00′ N., 110° 35′ W. Berkeley & Berkeley (1960) also report a specimen—" 1 mm. long, probably larval ", from 54° 30′ N., 152° 00′ W., which they call *L. uncinatus*; this is, I think, a most unusual record, and will have to be confirmed.

L. brevis was caught more often than *L. uncinatus*, though again across the breadth of the North Pacific and on occasion close to the northern boundary of the Sub-Tropical Zone (Text-fig. 53). This probably marks the limit of its northerly movement. Never more than one specimen was collected. All catches were in nets towed open in the top 290 metres of water, indicating that it is probably a surface water species. The first record of *L. brevis* from the North Pacific was made by Chamberlin (1919 as *L. parvum*) off the coast of Mexico (15° 58′ N., 98° 13′ W.) and subsequently Dales (1957) reported it from the California Current and Berkeley & Berkeley (1958) from 3° 03′ N., 101° 35′ W., and 10° 52′ N., 88° 02′ W.

MAUPASIA

M. caeca was found in all three hydrological zones (Text-fig. 54). This was expected because in the South Atlantic Ocean it is already known from warm and cold water regions (Tebble, 1960). On only two occasions were more than one specimen collected, and it appeared only in nets towed in the upper 525 metres of water. A number of these were closed in the deeper part of the layer indicating that *M. caeca* inhabits a considerable depth range.

M. caeca was first recorded from the North Pacific by Uschakov (1957*a*) from the

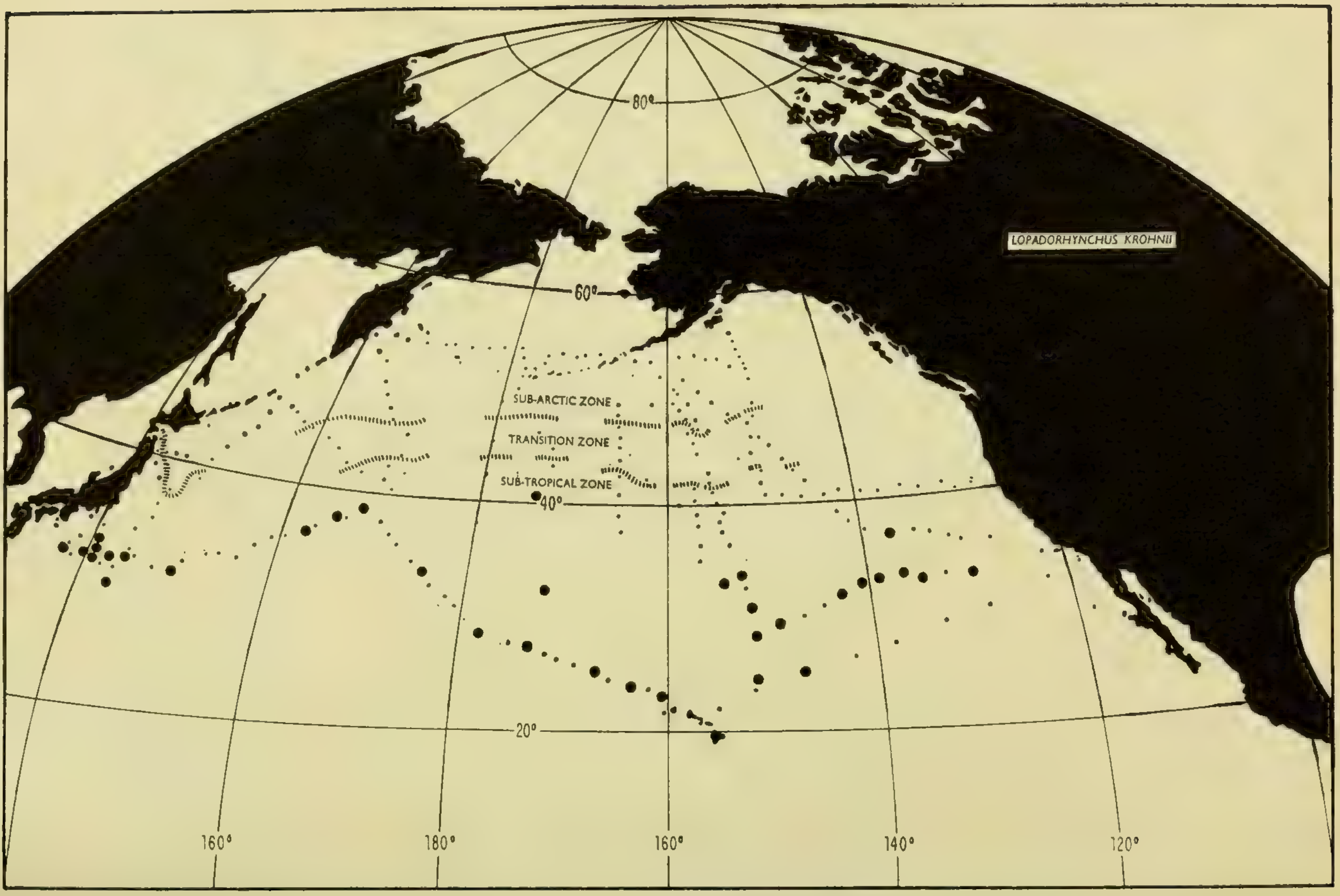
LOPADORHYNCHUS KROHNII
80°
60°
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
40°
20°
160°
180°
160°
140°
120°

FIG. 52. Occurrence of *Lopadorhynchus krohnii*.

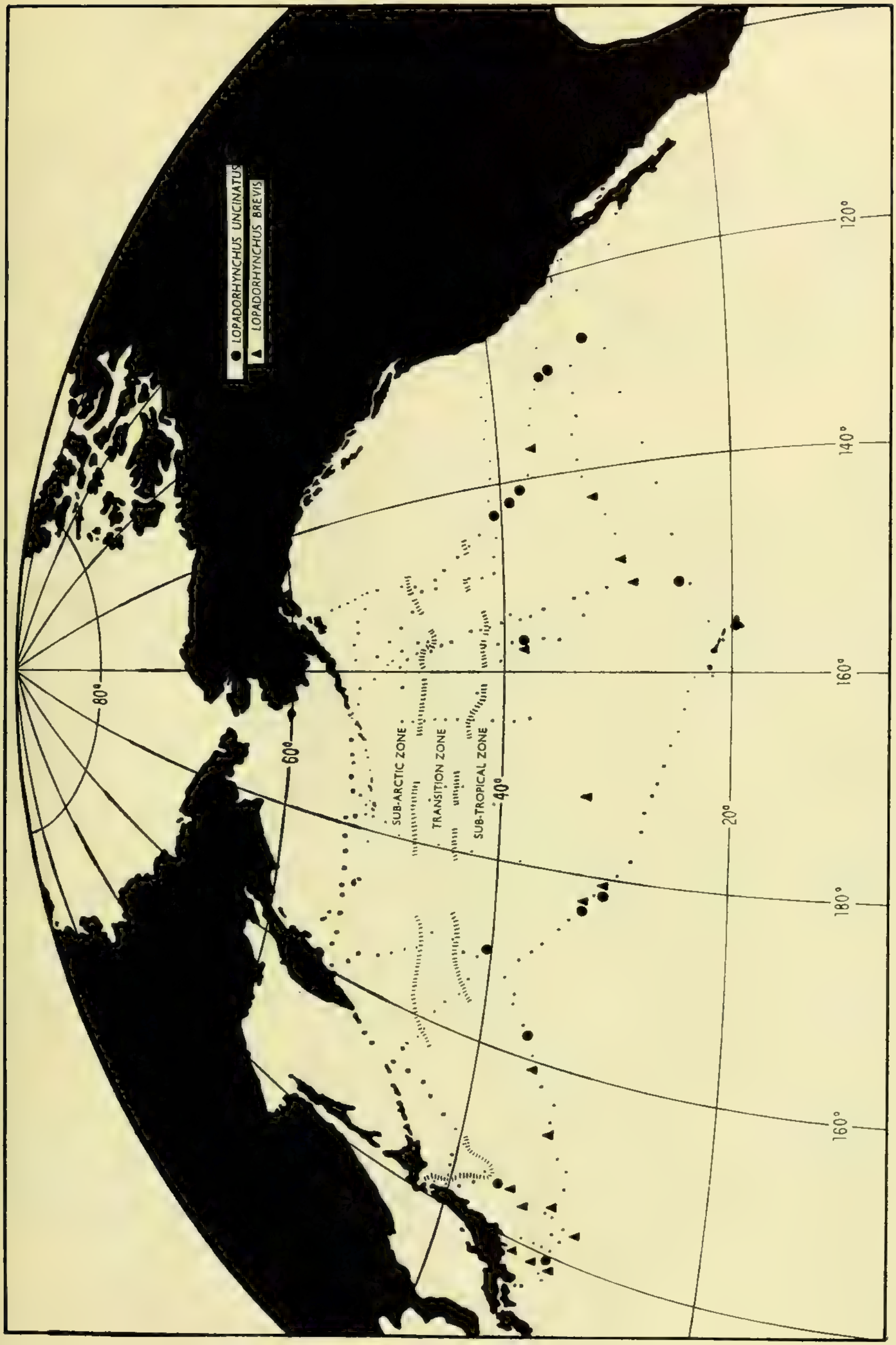
● LOPADORHYNCHUS UNCINATUS
▲ LOPADORHYNCHUS BREVIS
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 53. Occurrence of *Lopadorhynchus uncinatus* and *L. brevis.*

Transition Zone, 43° 08′ N., 156° 08′ E., and Berkeley & Berkeley (1958) later reported it from the Tropical Zone, 1° 58′ N., 83° 49′ W.

PEDINOSOMA

P. curtum was collected at only twelve stations, all east of 164° W., and in the Sub-Tropical Zone except for one record at the southern end of the Transition Zone (Text-fig. 54). It appeared only in nets towed open in the upper 415 metres of water: on only one occasion was more than one specimen collected. The only previous record of *P. curtum* from the North Pacific was made by Berkeley & Berkeley (1960) from 53° 32′ N., 151° 57′ W., and it is altogether too little known to draw conclusions about its distribution. Elsewhere in the world this species is not well known except in the North Atlantic where Reibisch (1895) found it only in Tropical and Sub-Tropical waters.

IOSPILINAE

PHALACROPHORUS

Two species of this genus are reported here, of which *P. pictus* appeared at numerous stations but *P. uniformis* at only one. This singular occurrence of *P. uniformis* at Stn. 126B of the Trans-Pacific Expedition (Text-fig. 55) consisted of fifty-three specimens, equivalent to sixty-two per 1,000 m^3 of water. This is a large number for any polychaete species, making the record particularly remarkable. Previously it was known from the North Pacific only through the records of Treadwell (1943 as *P. attenuatus*) from four stations made by the *Carnegie*, all south of the Transition Zone. In the Atlantic it is known only from Sub-Tropical and Tropical waters (Reibisch, 1895; Fauvel, 1916) and may be restricted to these zones in the North Pacific but more records will have to be obtained before this can be confirmed.

P. pictus was collected at numerous stations in the Sub-Arctic Zone, but at only one in the Sub-Tropical, Trans-Pacific Expedition Stn. 123A (Text-fig. 55). It would appear reasonable to consider this latter record an anomaly and treat the species as one restricted to the colder waters. There are, however, numerous literature records of *P. pictus* from Sub-Tropical waters which cannot be overlooked, these include Treadwell (1943, as *P. maculatus*), Uschakov (1957*a*) and Berkeley & Berkeley (1960), as well as others from the Sub-Arctic, Treadwell (1943), Berkeley & Berkeley (1958). It is clear therefore that the almost complete absence of this species from the collections reported here from the Sub-Tropical Zone was a result of its not being caught, rather than its not being there—a major hazard of plankton collecting.

Uschakov (1957*b*) has reported another species, *P. borealis*, from high Arctic waters in the North Pacific, beyond 76° N. This material is identical with that reported here as *P. pictus* and I consider the two species synonymous. It is possible, however, that the material reported as *P. borealis* represents a geographical race restricted to the colder water. This may also be applicable to the North Atlantic

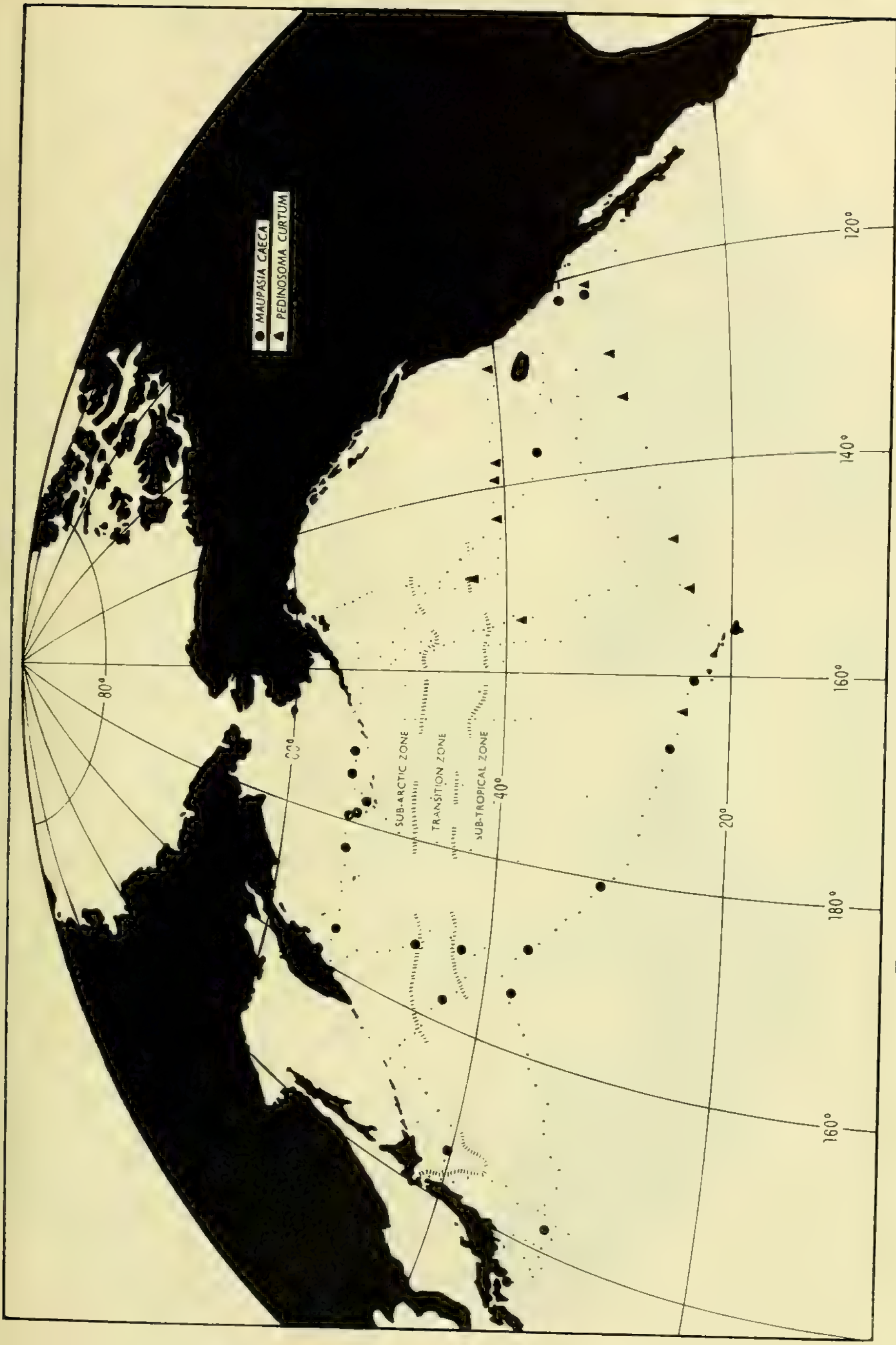
● MAUPASIA CAECA
▲ PEDINOSOMA CURTUM
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
80°
60°
40°
20°
120°
140°
160°
180°
160°

FIG. 54. Occurrence of *Maupasia caeca* and *Pedinosoma curtum*.

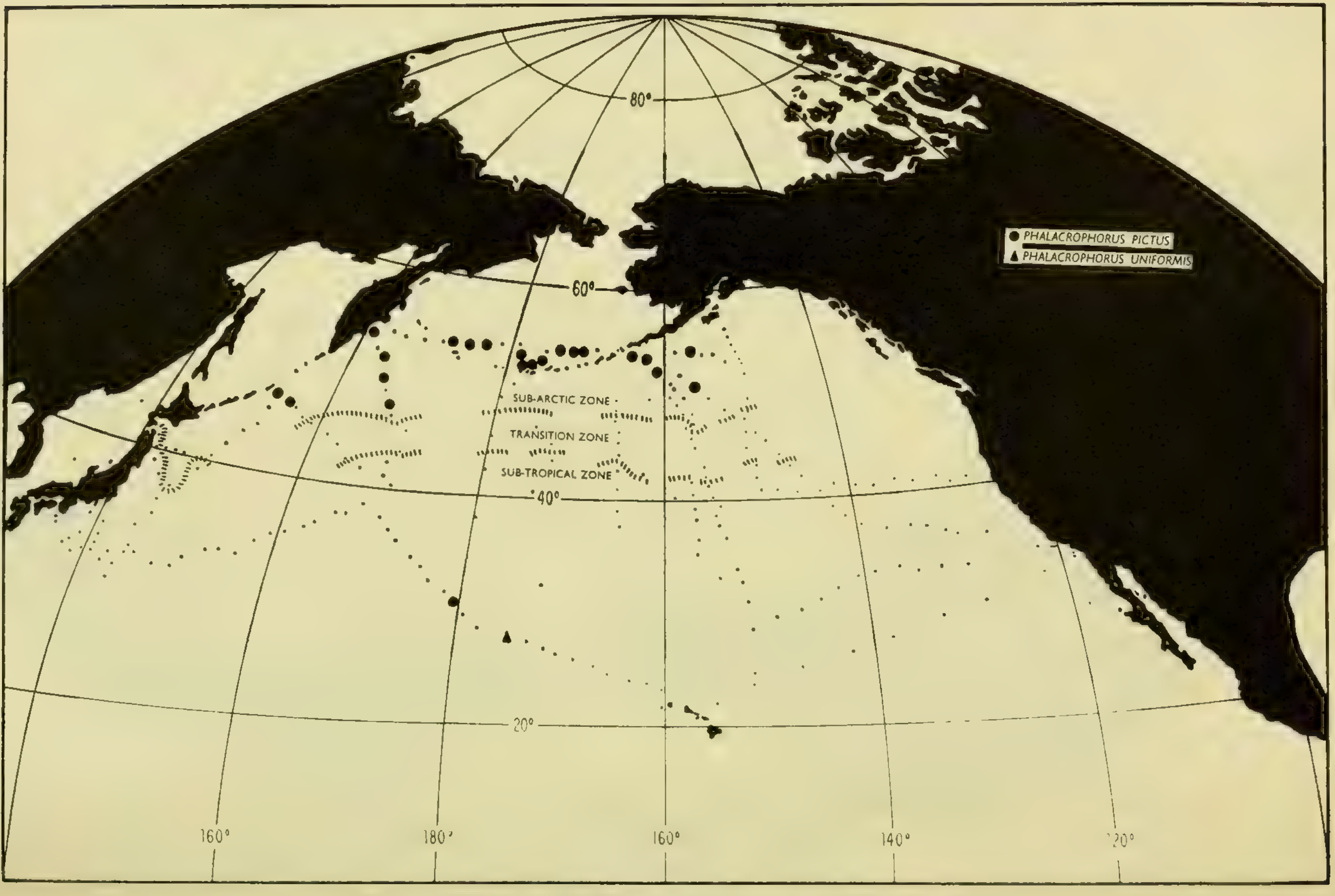
● PHALACROPHORUS PICTUS
▲ PHALACROPHORUS UNIFORMIS
80°
60°
40°
20°
SUB-ARCTIC ZONE
TRANSITION ZONE
SUB-TROPICAL ZONE
160°
180°
160°
140°
120°

FIG. 55. Occurrence of *Phalacrophorus pictus* and *P. uniformis*.

Ocean where *P. borealis* was first recorded by Reibisch (1895) entirely within Sub-Arctic waters but I would like to see material from a wider geographical range than at present available before drawing conclusions on this point. For the present, however, I think that *P. pictus* must be considered as potentially a cosmopolitan species.

ZOOGEOGRAPHICAL REVIEW

Thirty-three species are reported here of which twenty-one appear to have the northerly limit to their distribution in the North Pacific Ocean at either the northern boundary of the Sub-Tropical Zone or the southern boundary of the Sub-Arctic Zone; they are:

Tomopteridae	Alciopidae	Typhloscolecidae	Lopadorhynchinae
Tomopteris elegans	*Naiades cantrainii*	*Sagitella kowalewskii*	*Lopadorhynchus*
T. planktonis	*Vanadis longissima*	*Travisiopsis lobifera*	*L. uncinatus*
T. ligulata	*V. formosa*		*L. krohnii*
T. apsteini	*V. crystallina*		*L. brevis*
T. nisseni	*V. minuta*		
	V. tagensis		
	Rhynchonerella gracilis		
	R. petersii		
	R. mobii		
	Plotohelmis tenuis		
	Krohnia lepidota		

All of these effectively avoid the main body of the Sub-Arctic water mass in the Sub-Arctic Zone and, in that area of the North Pacific investigated, can be considered Sub-Tropical species. Because there is no definable " line of the Sub-Tropical Convergence ", between sub-tropical and sub-arctic water, stretching across the North Pacific (corresponding to the Sub-Tropical Convergence in the South Atlantic) but rather a Zone of Transition water, these species vary in the extent to which they penetrate beyond the northern boundary of the Sub-Tropical Zone. *Vanadis minuta* and *V. crystallina*, for example, were never found in Transition water but *Tomopteris elegans* and *Travisiopsis lobifera* can be collected there up to the border with the Sub-Arctic Zone. This does not warrant excluding the latter species from the list of Sub-Tropical forms. Indeed further collections may show that all species of this group can invade the Transition Zone, if only during certain seasons.

It has been noted that *Tomopteris planktonis*, *Rhynchonerella gracilis*, *Plotohelmis tenuis* and *Sagitella kowalewskii* may occasionally be found north of 45° N., principally in the North-East Pacific off the coast of British Columbia and Alaska. These species could be carried into this region by the Alaskan gyral (Text-fig. 2) and may be the most tolerant of the Sub-Tropical species. Boden *et al.* (1955) records similar northerly extensions for the distribution of the euphausiids *Nematoscelis difficilis*, *Nematobranchion flexipes* and *Stylocheiron longicorne*. Essentially sub-tropical and/or tropical in their distribution in the North Pacific as recorded by Brinton (1957) these species were found by Banner (1949) to extend to varying degrees north of the southern boundary of the Sub-Arctic off the slope waters of British Columbia. Bradshaw (1959) notes that a similar pattern is found in the foraminiferan *Orbulina universa*. It only remains for extensive collections from the area of the Alaskan gyral to be investigated to establish the geographical and seasonal extension of these and similar species. The fundamental feature of the distribution of all of them, however, is that they avoid the main body of oceanic water in the Sub-Arctic Zone.

It is possible that most of these twenty-one Sub-Tropical pelagic polychaetes occur also in Tropical waters in the Pacific Ocean but investigation of the extent of this will have to await further study. Bieri's (1959) analysis of chaetognath distribution in the North and South Pacific Oceans and Brinton's (1957) similar study on euphausiids draw attention to the great variety of distributional patterns which emerge from the study of a group over such immense areas. Involving so many different zoogeographical regions their work motivates a sense of caution towards any predictions whatsoever concerning distribution in the Pacific Ocean outside the region investigated.

Of the remaining twelve species five are cosmopolitan—*Tomopteris septentrionalis*, *Typhloscolex mülleri*, *Pelagobia longicirrata*, *Maupasia caeca* and *Phalacrophorus pictus*; one is known only from Sub-Arctic and Transition Zone waters of the North Pacific—*Tomopteris pacifica*; one occurs in all hydrological Zones in the Northern Hemisphere but avoids colder water in the Southern Hemisphere—*Rhynchonerella angelini*; and five are known from comparatively few records in the North Pacific and at the present time their distribution need not be examined further—*Travisiopsis levinseni*, *Tr. lanceolata*, *Tr. dubia*, *Phalacrophorus uniformis* and *Pedinosoma curtum*.

Of the Sub-Tropical species *Vanadis minuta* and *V. tagensis* are known only from the Pacific Ocean. It has been noted above that the latter is a deeper-water species, and many more collections from nets closing at depth in other oceans will have to be examined before it can be established as an exclusively Pacific Ocean species. *V. minuta* is a surface water form and one would expect it to have been reported from other oceans if it lived outside the Pacific. In fact this species is similar to *V. crystallina*, which is well known from the Atlantic, and they may have been confused in previously reported collections. I prefer, therefore, to delay suggesting that *V. minuta* is entirely restricted to the Pacific Ocean until more collections from other oceans have been examined.

Of the remaining nineteen species in this group seventeen are known from the North Atlantic Ocean entirely within Tropical and Sub-Tropical waters, although the records from there for a few of them are not numerous. The two which do not inhabit similar zoogeographical regions in the two oceans are *Tomopteris planktonis* and *Tomopteris nisseni*.

The absence of *T. planktonis* from the main body of Sub-Arctic water has been referred to above as entirely unexpected. Known from every other explored water mass in the world I can offer no satisfactory explanation of why this species, hitherto considered as cosmopolitan, should avoid this water. It may, of course, have been missed. Such a possibility, though remote, cannot be overlooked, and need not be accepted as invalidating any conclusions drawn for other species based on similar negative records: it may indeed represent one of the major hazards of reporting on the distribution of zooplankton.

T. nisseni inhabits Sub-Tropical and Tropical waters in the South Atlantic Ocean and similar water in the North Atlantic. In the latter, however, it also extends into Sub-Arctic and Arctic waters and I expected it to be present in the Pacific Sub-Arctic, from which it was, however, entirely absent. As an explanation of the extension of *T. nisseni* (and also *Tomopteris krampi*, *Rhynchonerella angelini* and *Travisiopsis lanceolata*) into the waters of higher latitudes in the North Atlantic, though absent from similar water in the South Atlantic, I suggested (Tebble, 1960) that they represented endemic antarctic elements in arctic waters. There being no endemic pelagic polychaetes in the North Atlantic, Sub-Arctic and Arctic it appeared to me that *T. nisseni* and *T. krampi* might represent there the endemic Antarctic species *T. carpenteri* and similarly *R. angelini* might represent *R. bongraini* and *Travisiopsis lanceolata* the southern hemisphere *Travisiopsis coniceps*. (It follows that the appearance of these four species in the Pacific Sub-Arctic was anticipated.) Only *Rhynchonerella angelini*, however, occurred in sufficiently large numbers there to lend credence to this suggestion, though *Tr. lanceolata* has been found there, but not in sufficient numbers to substantiate any conclusions at present which must await further collections. Not only was *T. nisseni* not present in the Sub-Arctic, but *T. krampi* was not present in any of the samples I examined from the North Pacific, and although Dales (1955) reported it from Monterey Bay, he did not find it in the California Current (Dales, 1957). Disregarding then, for the present, *T. krampi*, it is necessary only to find an explanation for the absence of *T. nisseni* from the Sub-Arctic. This appears to me to be possible through the presence there, and in the Transition Zone only, of *T. pacifica*. This species may be considered as restricted to the Pacific Sub-Arctic and Transition Zones (whether or not it extends into high polar waters is not relevant at present) and it may have replaced *T. nisseni* (and *T. krampi*) in these waters as representative of the endemic antarctic elements—as much as we have seen *Rhynchonerella angelini* represents *R. bongraini*. It appears, therefore, as if *T. nisseni* extends into waters of higher latitudes only when there are no endemic tomopterid elements present. This is the conclusion that can be drawn from the evidence of distribution in the North Pacific and Atlantic Oceans. It is at the same time a reminder that animals are not necessarily the slaves of hydrological characteristics or water masses.

Of the thirty-three species reported here from the North Pacific all except three are also known from the Atlantic (the three exceptions *Tomopteris pacifica, Vanadis tagensis* and *Vanadis minuta* have been examined above). It is significant that most of the species making up such a high percentage, 91%, common to both areas, occur in abundance rather than as scattered isolated elements. Specimens of some species, however, in particular *Tomopteris planktonis, Typhloscolex mülleri* and *Vanadis longissima*, have characteristics which permit immediate separation of the Pacific from the Atlantic forms. If these particular specimens have been collected as isolated catches they could have been described as new species; but if they are examined in the light of the wide range over which they, and closely related forms, are known to exist, and in relation to the hydrological boundaries restricting their distribution, the problem can be viewed less empirically. Thus there is abundant evidence that the species which vary distinctively in form, range, within their hydrological limits, throughout the South Pacific into the Indian and Atlantic Oceans ; in the North Pacific they either meet a hydrological barrier which restricts their movement northwards, or enter a circulation which can be an effective isolating mechanism.

Thus, *T. planktonis* ranges throughout the southern hemisphere to the North Pacific, where it is restricted in its distribution at the southern boundary of the Sub-Arctic Zone. It is thus at the very edge of its range that morphological differences occur in some members of the population. *Typhloscolex mülleri* is very well known as a cosmopolitan polychaete, but it is only in the Sub-Arctic waters of the North Pacific that a cold water ecotype has been found. Although abundant in the Antarctic, no isolating mechanism appears to have been effective to produce a comparable anti-boreal population. It is apparent that, within the Sub-Arctic Zone, the necessary isolating circulation has been effective, and it would be of the greatest interest if the hydrographers could indicate the limits of such a circulation In the case of *T. mülleri* this must be different from that applying to an endemic sub-arctic species, for in this species the cold water ecotype is restricted but the other members of the population are not.

The presence of a few specimens of *V. longissima* in and near the Transition Zone which can be instantly separated from other members of the species by the possession of black markings on the eyes suggests that we might be dealing here with a separate physiological race. At the southern extremity of its distribution in the southern hemisphere *V. longissima* meets the endemic antarctic *V. antarctica*. These two are very similar morphologically and may, in fact be semi-sympatric species. Such ecological allopatry combined with genetical contiguity probably represents a stage towards complete separation of the species. The physiological race (?) here reported from the North Pacific may be an earlier step in this process.

McGowan (1960) has examined the distribution of the aberrant planktonic worm *Pocobius meseres* Heath, in the North Pacific Ocean. The systematic relationships of this animal are problematical and I do not intend to comment here on whether or not it is a polychaete ; it may be noted, however, that McGowan found *P. meseres* mainly in the Sub-Arctic and Transition Zones. A few specimens he found to the south of the latter region he considered non-endemic, having been carried in from the north.

APPENDIX I

The actual number of specimens collected at each station is recorded here. When only a fraction of a sample was examined this is indicated and allowance made in the column headed " Volume of water filtered, m^3 ".

TABLE I

Stns. in the Sub-Tropical and Transition Zones

TRANS-PACIFIC EXPEDITION	Stns. 1 to 18. Stns. 51 to 60. Stns. 70, 74 to 77, 79 to 143.
NORTHERN HOLIDAY EXPEDITION	Stns. 2 to 18. Stns. 44 to 66.
CHINOOK EXPEDITION	Stns. 1 to 5. Stns. 7 to 9.
P.O.F.I. *Hugh M. Smith*, CRUISE NO. 30	Stns. 26 to 32. Stns. 44 to 79. Stns. 87 to 102.

TABLE II

Stns. in the Sub-Arctic Zone

TRANS-PACIFIC EXPEDITION	Stns. 19 to 50. Stns. 61 to 69, 71 to 73, 78.
NORTHERN HOLIDAY EXPEDITION	Stns. 19 to 40.
CHINOOK EXPEDITION	Stn. 6.
P.O.F.I. *Hugh M. Smith*, CRUISE NO. 30	Stns. 37. Stns. 80 to 86.

TABLE III

Dept. of Oceanography, University of Washington, Seattle, Washington, Collections

CRUISE BB–199—MWT : 50 records.
CRUISE BB–202—MWT : 3 records.

TABLE I.—*Species Collected at Stns. in the Sub-Tropical and Transition Zones**

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³)	*Tomopteris elegans*	*Tomopteris septentrionalis*	*Tomopteris planktonis*	*Tomopteris ligulata*	*Tomopteris nisseni*	*Tomopteris apsteini*	*Tomopteris* not identifiable	*Naiades cantrainii*	*Vanadis formosa*	*Vanadis crystallina*	*Vanadis minuta*	*Vanadis longissima*	*Vanadis lagensis*	*Rhynchonerella gracilis*	*Rhynchonerella mobii*	*Rhynchonerella petersii*	*Rhynchonerella angelini*	*Plotohelmis tenuis*	*Krohnia lepidota*	Alciopid fragments	*Typhloscolex mulleri*	*Sagitella kowalewskii*	*Travisiopsis lobifera*	*Lopadorhynchus brevis*	*Lopadorhynchus uncinatus*	*Lopadorhynchus krohnii*	*Pelagobia longicirrata*	*Maupasia caeca*
TRANS-PACIFIC EXPEDITION																																	
1A	33° 57·5′	122° 28′ W.	23.vii.53	0–145	444		32																6		×								
B	,,	,,	,,	0–330	816	2	19																1		×	1	1	1				1	1
3A	35° 04·9′	127° 37·7′ W.	25.vii.53	0–165	531	47						153									1		1					1					
B	,,	,,	,,	0–320	1,130	122	1					71						1					2				1	1					
4A	35° 46·8′	130° 02·5′ W.	26.vii.53	0–165	525	51																			×								
B	,,	,,	,,	165–330	555	72			3									1							×								
C	,,	,,	,,	330–495	555	1																				1	1						
D	,,	,,	,,	0–1,015	2,795	163	8					32				1									×	1				1		5	
5A	35° 54·0′	131° 44·0′ W.	27.vii.53	0–135	445	10	1					9											1					1					
B	,,	,,	,,	0–355	1,035	44	1					3	1			1		2								1							
6A	36° 09·2′	133° 20·0′ W.	27.vii.53	0–115	411	131							2	1							1				×								
B	,,	,,	,,	0–260	970	125		1					1	3	1																		
7A	36° 21·8′	134° 53·0′ W.	28.vii.53	0–170	251	64				2				1					1						×		1						
B	,,	,,	,,	170–340	464	64																				3							
C	,,	,,	,,	340–510	464					1		1															1						
D	,,	,,	,,	510–680	464	13																					1					1	
E	,,	,,	,,	0–1,035	2,120	126	9																			3	2					3	
8A	36° 44·0′	137° 23·7′ W.	29.vii.53	0–145	500	90								1		1									×		2		1		2		1
B	,,	,,	,,	0–310	1,212	306											2		3			3					2				3		
9A	37° 00·0′	140° 01·5′ W.	29.vii.53	0–170	524	142	1	1				43	1			1	2		2			1		1		1	1	1					
B	,,	,,	,,	170–340	705	4																				1						2	
C	,,	,,	,,	340–510	705	1																											
D	,,	,,	,,	510–680	705	1																											
E	,,	,,	,,	0–1,035	2,386	272	1					77	1	1											×	1	1					6	
10A	38° 22·3′	141° 23·2′ W.	31.vii.53	0–120	362	144						14									2	1			×	2						1	
B	,,	,,	,,	0–230	1,038	172		1													2									1			
11A	39° 35·6′	142° 33·0′ W.	1.viii.53	0–170	801	1,058						191									4				×	1		1		1			
B	,,	,,	,,	170–340	889	35												1								5							
D	,,	,,	,,	510–680	889	32	1											1					1		×	3	4					3	
E	,,	,,	,,	680–850	889							5															2					10	
F	,,	,,	,,	0–1,280	4,815	141	2						1													2	2	1				14	
12A[1]	40° 26·9′	143° 32·0′ W.	2.viii.53	0–170	639	654						108					1				1				×	1		1				1	
B	,,	,,	,,	170–340	667																					1							
C	,,	,,	,,	340–510	667			2																		5	2						
D	,,	,,	,,	510–680	667	6	9					13														2	2	1				1	
E[1]	,,	,,	,,	680–850	667							5									1				×							12	
F	,,	,,	,,	0–1,280	3,680	281								1								3	1		×	3	3			1		10	

* For footnotes see p. 483.

TABLE I—*contd.*

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³)	*Tomopteris elegans*	*Tomopteris septentrionalis*	*Tomopteris planktonis*	*Tomopteris ligulata*	*Tomopteris nisseni*	*Tomopteris apsteini*	*Tomopteris* not identifiable	*Naiades cantrainii*	*Vanadis formosa*	*Vanadis crystallina*	*Vanadis minuta*	*Vanadis longissima*	*Vanadis tagensis*	*Rhynchonerella gracilis*	*Rhynchonerella mobii*	*Rhynchonerella petersii*	*Rhynchonerella angelini*	*Plotohelmis tenuis*	*Krohnia lepidota*	Alciopid fragments	*Typhloscolex mülleri*	*Sagitella kowalewskii*	*Travisiopsis lobifera*	*Lopadorhynchus brevis*	*Lopadorhynchus uncinatus*	*Lopadorhynchus krohnii*	*Pelagobia longicirrata*	*Maupasia caeca*
13A	41° 53·8′	145° 13·0′ W.	3.viii.53	0–125	431	205	6					3														4						12	
B	,,	,,	,,	0–340	876	393	7					123													×	3		2				10	
14A[1]	42° 57·5′	146° 14·8′ W.	3.viii.53	0–175	663	142	4			1		3														1						2	
B	,,	,,	,,	0–380	254	47	9					27														2							
15A	44° 01·9′	147° 29·2′ W.	4.viii.53	0–170	586	16						24														1		1					
B	,,	,,	,,	135–350	332							16														1		1					
16A	44°59′	148° 46·5′ W.	4.viii.53	0–165	1,202	4	4					101														3						1	
B	,,	,,	,,	165–330	685																					1	1						
16C	44° 59′	148° 4·65′ W.	4.viii.53	330–495	685		1																										
D	,,	,,	,,	495–660	685							3																				3	
E[2]	,,	,,	,,	0–980	821		1					46														1						7	
17A	46° 00·0′	149° 54·0′ W.	5.viii.53	0–135	441	48	91																										
B	,,	,,	,,	160–295	370	9	5					20														4							
18A	47° 14·0′	151° 43·0′ W.	6.viii.53	0–169	443		4					19										1				1							
B[3]	,,	,,	,,	0–318	1,295		44																			2							
51A	45° 05·5′	170° 08·5′ E.	7.ix.53	0–145	440		7					76					1		1		1												
B	,,	,,	,,	0–330	934		18					64										2				16							
52A	43° 28·1′	170° 37·3′ E.	8.ix.53	0–155	500		19	1				77														2							
B	,,	,,	,,	155–260	370		9					18											4		×	12	3						
53A	42° 07·9′	169° 28·1′ E.	8.ix.53	0–190	933	3						19	1			3					1		3		×		3						
B	,,	,,	,,	140–295	500							30										1	1			2							1
C	,,	,,	,,	290–545	425							1																				2	
54A	40° 34·5′	170° 02·3′ E.	9.ix.53	0–170	810	8			1			82				1	2					2	1		×			1					
B	,,	,,	,,	170–340	705							11								1					×	17	2					1	
C	,,	,,	,,	340–510	705							1														10	2	1				2	
D[4]	,,	,,	,,	0–1,015	3,650	1	2	1				14														9	9			1		4	
55A	41° 19·0′	168° 20·2′ E.	9.ix.53	0–169	463	1						9			1										×								
B	,,	,,	,,	153–288	388							30											1		×	8		1					
56A	41° 49·0′	166° 38·6′ E.	10.ix.53	0–135	530							29					1				1			1			1	2					
B	,,	,,	,,	0–258	1,053	8						35							1	1					×	9		1					

TABLE I—*contd.*

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³)	*Tomopteris elegans*	*Tomopteris septentrionalis*	*Tomopteris planktonis*	*Tomopteris ligulata*	*Tomopteris nisseni*	*Tomopteris apsteini*	*Tomopteris* not identifiable	*Naiades cantrainii*	*Vanadis formosa*	*Vanadis crystallina*	*Vanadis minuta*	*Vanadis longissima*	*Vanadis lagensis*	*Rhynchonerella gracilis*	*Rhynchonerella mobii*	*Rhynchonerella petersii*	*Rhynchonerella angelini*	*Plotohelmis tenuis*	*Krohnia lepidota*	Alciopid fragments	*Typhloscolex mulleri*	*Sagitella kowalewskii*	*Travisiopsis lobifera*	*Lopadorhynchus brevis*	*Lopadorhynchus uncinatus*	*Lopadorhynchus krohnii*	*Pelagobia longicirrata*	*Maupasia caeca*
57A	42° 41·4′	164° 57·1′ E.	11.ix.53	0–160	487		27					52														3	3						
B[7]	,,	,,	,,	144–312	610		8					32														5							
C[7]	,,	,,	,,	318–491	650																	1				2						24	
58A	43° 23·4′	163° 12·9′ E.	12.ix.53	0–164	499		3					19													+	1							
B	,,	,,	,,	1153–18	390		12					90														12	1					2	1
59A	44° 06·0′	161° 39·0′ E.	13.ix.53	0–163	955							36										1				5							
B	,,	,,	,,	163–326	815							13											1		×	6	1						
C	,,	,,	,,	326–490	815							6														1	1					1	
D	,,	,,	,,	490–653	815							4																				26	
E[6]	,,	,,	,,	0–980	3,890		2					34														5	7					42	
60A	44° 46·1′	159° 54·9′ E.	13.ix.53	0–129	464		1					8														7	1						
B	,,	,,	,,	0–258	1,059		34	21				10											1		×	25							
70A[4]	39° 44·0′	148° 24·0′ E.	19.ix.53	0–165	449							7												1			3	1					
E[6]	,,	,,	,,	0–1,016	3,442		2					56					1								×	5	2	1					
74A	41° 22·2′	142° 18·3′ E.	22.ix.53	0–118	459		2					2														3							
B	,,	,,	,,	160–288	1,110		15	3				5										2				2							
75A	40° 54·6′	142° 18·1′ E.	28.ix.53	0–106	505							10																					
B	,,	,,	,,	121–225	444		14					61										1				1							
76A	39° 56·4′	143° 38·5′ E.	28.ix.53	0–163	1,200			3									1		4					2	×	5	6	1				5	
D	,,	,,	,,	490–652	1,424		4																			1						4	
E	,,	,,	,,	0–980	3,680	1	8	2			1	20							2						×	4	4					5	
77A	38° 58·6′	144° 51·0′ E.	29.ix.53	0–124	569							36					2		4							3							
B[6]	,,	,,	,,	149–318	1,054	3	1					24														2							
79B	26° 23·2′	145° 30·4′ E.	30.ix.53	139–324	314	5				1		7																		1			
C	,,	,,	,,	318–720	555							5															1					1	
80A	35° 04·5′	145° 07·5′ E.	1.x.53	0–112	430	7			4			9				1	3				1		1	2	×	1	2	2	1				
B	,,	,,	,,	0–258	1,020	17		11		1					1		2		2		2				×	1		2					
81A	34° 06·0′	144° 36·5′ E.	2.x.53	0–127	450							9				1									×			1	1				
B	,,	,,	,,	147–318	444	3				4		10																					
82A	32° 59·6′	144° 15·0′ E.	2.x.53	0–129	464							3				2									×	1	1						
83A	31° 08·3′	143° 41·0′ E.	3.x.53	0–164	536							1											1		×	1	2						
B	,,	,,	,,	0–225	1,662							9					1	1		1			1		×	1	1	3					

TABLE 1—*contd.*

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³)	*Tomopteris elegans*	*Tomopteris septentrionalis*	*Tomopteris planktonis*	*Tomopteris ligulata*	*Tomopteris nisseni*	*Tomopteris apsteini*	*Tomopteris* not identifiable	*Naiades cantrainii*	*Vanadis formosa*	*Vanadis crystallina*	*Vanadis minuta*	*Vanadis longissima*	*Vanadis lagensis*	*Rhynchonerella gracilis*	*Rhynchonerella mobii*	*Rhynchonerella petersi*	*Rhynchonerella angelini*	*Plotohelmis tenuis*	*Krohnia lepidota*	*Alciopid* fragments	*Typhloscolex mülleri*	*Sagitella kowalewskii*	*Travisiopsis lobifera*	*Lopadorhynchus brevis*	*Lopadorhynchus uncinatus*	*Lopadorhynchus krohnii*	*Pelagobia longicirrata*	*Maupasia caeca*
84A	30° 09·0′	143° 15 7′ E.	3.x.53	0–153	468							16				3	1							1	×	1	2	1	1		1		
B	,,	,,	,,	135–300	444							14													×								
C	,,	,,	,,	369–525	14,80																					1							
85A*	31° 23·4′	141° 23·6′ E.	4.x.53	0–153	440	1		3				4			3		1		1						×		3	8					
B	,,	,,	,,	139–258	1,166							8														1							
86A*	32° 26·8′	140° 36·6′ E.	5.x.53	0–153	436	1		1				2				1				1					×	1	14	6			2		
B	,,	,,	,,	0–369	1,240	3		4				17				5			1	1				1	×	3	5	8			2		
87A	33° 23·5′	140° 27·9′ E.	6.x.53	0–177	450	1		1	1			8			1	4								1	×	1	5	9			1		
B*	,,	,,	,,	0–397	735	1						33			1	1				1					×	4	7	10					
88A*	34° 18·8′	140° 11·0′ E.	6.x.53	0–164	465	2		2				6				3				1	1				×	1	6						
89A	34° 21·5′	138° 40·5′ E.	15.x.53	0–138	703			1			1	4	1			4			1		2				×	3	1		1				
B	,,	,,	,,	120–260	426	3				1		4													×								
91A*	33° 16·0′	138° 10·0′ E.	16.x.53	0–150	420			1		2		4											1	1	×	2							
B	,,	,,	,,	0–290	870							8					1						1		×	3	1		1				
92A	32° 45·0′	137° 47·5′ E.	16.x.53	0–110	432			2				12							1	1					×	6	3						
B	,,	,,	,,	0–295	1,058							9				1			2						×	6	1						
93A*	33° 25·2′	135° 06·0′ E.	24.x.53	0–110	565							4							1						×	2	3					1	1
94A	32° 59·5′	135° 57·0′ E.	24.x.53	0–140	492																				×	4							
B	,,	,,	,,	140–310	444	4						3														1							
95A	32° 22·8′	137° 06·7′ E.	24.x.53	0–110	419	1	1	1											1	1				1	×	2					2		
B	,,	,,	,,	133–290	370							5														1							
C	,,	,,	,,	295–520	1,572							3																					
96A*	31° 44·3′	138° 00·0′ E.	25.x.53	0–115	434							4				1					1			1	×	11	1		1			1	
B	,,	,,	,,	110–300	1,147	2						5			1										×							1	
97A	32° 02·3′	139° 25·1′ E.	25.x.53	0–170	756						1	21	1											4	×	3	6				1		
B	,,	,,	,,	170–340	1,424	3						3														1							
C	,,	,,	,,	140–510	1,424							8															6					1	
D	,,	,,	,,	210–680	1,424							7																					
E	,,	,,	,,	0–1015	4,345			1				5				1									×		1			1			
98A	32° 03·3′	141° 04·1′ E.	26.x.53	0–155	421			1				4												1			7				1		
B	,,	,,	,,	0–288	770	3	3									1	1	1							×		2	6			2		
99A	31° 55·3′	142° 11·7′ E.	26.x.53	0–150	423	1						7	1			1	1				1				×		8	54			3		1
B	,,	,,	,,	160–335	426	4		4			1	10						1					1		×		1						

TABLE I—*contd.*

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³)	*Tomopteris elegans*	*Tomopteris septentrionalis*	*Tomopteris planktonis*	*Tomopteris ligulata*	*Tomopteris nisseni*	*Tomopteris apsteini*	*Tomopteris* not identifiable	*Naiades cantrainii*	*Vanadis formosa*	*Vanadis crystallina*	*Vanadis minuta*	*Vanadis longissima*	*Vanadis lagensis*	*Rhynchonerella gracilis*	*Rhynchonerella mobii*	*Rhynchonerella petersii*	*Rhynchonerella angelini*	*Plotohelmis tenuis*	*Krohnia lepidota*	*Alciopid fragments*	*Typhloscolex mülleri*	*Sagitella kowalewskii*	*Travisiopsis lobifera*	*Lopadorhynchus brevis*	*Lopadorhynchus uncinatus*	*Lopadorhynchus krohnii*	*Pelagobia longicirrata*	*Maupasia caeca*
100A	32° 14·0′	144° 02·1′ E.	29.x.53	0–115	464	1						5			1	1									×	3	3	5			1		
101A	32° 10·0′	145° 53·0′ E.	29.x.53	0–165	418			2				11			2		1						1		×	2	1	2	1				
B	,,	,,	,,	140–275	426							11								1						1		18					
102A	31° 57·0′	147° 53·5′ E.	30.x.53	0–155	321			1				4		1	1	1	6		1						×			1					
103A	31° 49·1′	149° 58·0′ E.	30.x.53	0–175	458	5		2	1			10				3	1		1						×	1	4	12			1		
B	,,	,,	,,	145–290	426	3		7	1	2		8			1			1					2		×								
104A	32° 36·8′	151° 27·4′ E.	31.x.53	0–140	373	8		1				13	2				8				1						3	1					
B	,,	,,	,,	175–265	388	5		6	1	3		5						1					3		×			30					
105A	33° 09·5′	153° 00·0′ E.	31.x.53	0–175	362	6		3			1	14				1	2						1		×	3	4	6					
B	,,	,,	,,	0–290	715	2		8				14			2	3	2						2		×		8		1				
106A	33° 33·9′	154° 29·1′ E.	1.xi.53	0–165	425							8				1	3						1	1	×	2	3						
B	,,	,,	,,	130–300	703							12											1		×			1					
107A	34° 07·0′	156° 11·0′ E.	2.xi.53	0–160	553							1				7	2		1						×			5					
B	,,	,,	,,	0–305	986	1						3				1	1											4					
C[10]	,,	,,	,,	0–530	3,150												1				1												
108A	34° 44·8′	157° 39·5′ E.	2.xi.53	0–115	491			1				15			1				2			1	1		×	13	10	6					
B	,,	,,	,,	130–300	1,202							7						2								2	2						
109A	35° 14·0′	159° 04·0′ E.	3.xi.53	0–120	446			1	1		1	13		1		3			2			1			×	3	2	3	1			1	
B	,,	,,	,,	0–330	1,012	7	1	4	1			12				2			1						×	1	2	1					
110A	35° 40·0′	160° 43·0′ E.	3.xi.53	0–85	486	7	7		1			11			1	1	1		6					1	×	3	5	12					
111A	36° 04·0′	162° 13·5′ E.	4.xi.53	0–155	411	1						9	1	1							1			1				2					
B	,,	,,	,,	0–275	871							61	1			1	1		2		1			4	×	3	3	1		1	2		
112A	36° 35·0′	163° 46·0′ E.	4.xi.53	0–135	499	5		1					1		1	5			1						×		1	1					
B	,,	,,	,,	160–275	462																				×	8	1						
113A	37° 28·0′	165° 16·0′ E.	5.xi.53	0–150	380		1					4				4	1		1						×	1	1						
B	,,	,,	,,	0–315	842		3									3	1							1	×			1			1	1	
114A	37° 53·5′	166° 56·7′ E.	5.xi.53	0–160	462	2			3							4	1	1							×								
B	,,	,,	,,	150–385	444	1																				1							
115A	38° 31·5′	168° 31·5′ E.	6.xi.53	0–165	394	1						7				4	1		1		1			1	×		1	1					1
B	,,	,,	,,	0–330	806	4		7				21			1	4	1		1				1	1	×	2			1		1		
116A	37° 40·5′	170° 06·2′ E.	7.xi.53	0–105	415	1		2	2			5				1			4		1				×		1	1					
B	,,	,,	,,	0–280	920	4	1	3	2			1		1		1	1		1						×	1	1	1					

TABLE I—*contd.*

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³)	*Tomopteris elegans*	*Tomopteris septentrionalis*	*Tomopteris planktonis*	*Tomopteris ligulata*	*Tomopteris nisseni*	*Tomopteris apsteini*	*Tomopteris* not identifiable	*Naiades cantrainii*	*Vanadis formosa*	*Vanadis crystallina*	*Vanadis minuta*	*Vanadis longissima*	*Vanadis lagensis*	*Rhynchonerella gracilis*	*Rhynchonerella mobii*	*Rhynchonerella petersii*	*Rhynchonerella angelini*	*Plotohelmis tenuis*	*Krohnia lepidota*	*Alciopid* fragments	*Typhloscolex mülleri*	*Sagitella kowalewskii*	*Travisiopsis lobifera*	*Lopadorhynchus brevis*	*Lopadorhynchus uncinatus*	*Lopadorhynchus krohnii*	*Pelagobia longicirrata*	*Maupasia caeca*
117A	36° 35·0′	171° 26·0′ E.	7.xi.53	0–145	415	3	4									1			1						×								
B	"	"	"	150–335	1,092																	1											
C	"	"	"	320–600	1,258							2														1	1	1					1
118A	35° 36·8′	172° 43·7′ E.	8.xi.53	0–155	387	1						20	1		1	2	1		2							1	4	4					
B[11]	"	"	"	0–345	877	24		5		2		16						1					1		×	5	1	1					
119B	34° 30·5′	174° 04·0′ E.	8.xi.53	310–370	444	9		3	5	1								1	1	1					×								
120A	33° 23·1′	175° 13·2′ E.	9.xi.53	0–140	466	9			1	3			1		1	1	1		1					3	×	1	1	1	1		1		
B	"	"	"	145–320	407			1	6			2											1				2	2					
C	"	"	"	355–535	629		1					5																					
121A	32° 34·1′	176° 44·8′ E.	10.xi.53	0–140	453	10		5	1			3	1			1					1			1	×	1	1	1	1	2			
B	"	"	"	135–220	426	2		2				8						1	1				1		×		1						
123A[14]	30° 36·8′	179° 30·0′ E.	11.xi.53	0–130	524				1			1	1	1		9	1				1			1	×		1		1	1			1
B	"	"	"	130–260	407	1			3	1								1	1						×								
124A	29° 39·0′	179° 09·8′ W.	10.xi.53	0–135	677	6						6				4							1	1	×	1							
B	"	"	"	150–325	1,147	2						3															1						
C	"	"	"	335–515	1,332																												
125A	28° 38·0′	178° 01·8′ W.	11.xi.53	0–142	457	1			1		1	3		1		3			2	1					×	2	2				2		
B	"	"	"	146–349	1,147							9						1							×								
126A	27° 58·2′	175° 01·9′ W.	13.xi.53	0–131	408							7			1	2			1						×		2						
B[15]	"	"	"	0–259	858	4		3				9			1	4	1				1	3			×		2						
127B	27° 32·0′	173° 28·5′ W.	13.xi.53	146–295	705	2		2	5		2	3													×	1	2				2		
128B	26° 58·8′	171° 55·1′ W.	14.xi.53	153–259	1,020	4				2	1	4			1			1		1			1	1	×	1	1						
129A	26° 28·5′	170° 23·0′ W.	14.xi.53	0–109	411	12		1							1										×		1						
B	"	"	"	0–264	920	13		10	4	1		2				4					1			1	×	1	1						
130B	25° 52·2′	168° 42·7′ W.	15.xi.53	123–290	704	11		1			1	2									1				×	4	2						
131A	25° 12·4′	166° 56·0′ W.	15.xi.53	0–123	526				1			9		1		8					1				×		4						
B	"	"	"	0–307	900	7		4	3			21													×		4				1		1
132A	24° 38·0′	165° 22·0′ W.	16.xi.53	0–181	398			1				2													×	1	1						
B	"	"	"	153–345	850	2		4				2			1	1									×		4						
133A[16]	23° 55·3′	163° 39·6′ W.	17.xi.53	0–144	457							3		3		5									×		1						
B	"	"	"	0–277	968	1						7			1	7					1				×		1				1		

TABLE I—*contd.*

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³)	*Tomopteris elegans*	*Tomopteris septentrionalis*	*Tomopteris planktonis*	*Tomopteris ligulata*	*Tomopteris nisseni*	*Tomopteris apsteini*	*Tomopteris* not identifiable	*Naiades cantrainii*	*Vanadis formosa*	*Vanadis crystallina*	*Vanadis minuta*	*Vanadis longissima*	*Vanadis lagensis*	*Rhynchonerella gracilis*	*Rhynchonerella mobii*	*Rhynchonerella petersii*	*Rhynchonerella angelini*	*Plotohelmis tenuis*	*Krohnia lepidota*	*Alciopid* fragments	*Typhloscolex mülleri*	*Sagitella kowalewskii*	*Travisiopsis lobifera*	*Lopadorhynchus brevis*	*Lopadorhynchus uncinatus*	*Lopadorhynchus krohnii*	*Pelagobia longicirrata*	*Maupasia caeca*
134A	23° 26·3′	161° 49·6′ W.	17.xi.53	0–129	441							2	1			3					1				×	2	1						
B	,,	,,	,,	0–283	1,015	3		1				4			1	5					1				×	2	3						
153A	22° 50·0′	160° 05·6′ W.	18.xi.53	0–151	405	2						3				3				1					×	1		1					1
B	,,	,,	,,	146–290	1,202	2		2	3			6									1						1				1		2
136A	21° 42′	156° 19′ W.	21.xi.53	0–375	793	2						5			1	8									×	1	1						
137A[18]	23° 05′	152° 02′ W.	22.xi.53	0–320	714	14										4			1		1	1	1		×	1	1						
138A[18]	24° 27′	147° 32′ W.	23.xi.53	0–345	769	7			2			7	1			5				1	1			1	×		3				2		
139A	25° 48′	142° 43′ W.	24.xi.53	0–320	895	5		1	2	1						1			1						×	1	2						
140A	26° 57′	138° 22′ W.	25.xi.53	0–325	645	3		1	1						1	2				1					×	3	6	1					
141A[18]	28° 14′	133° 38′ W.	26.xi.53	0–325	641	3		2				4		1		2								1	×	1	8						
142A[18]	29° 31′	128° 47′ W.	27.xi.53	0–300	788	4		5					1						1						×	1	1						
143A[18]	31° 00′	123° 00′ W.	28.xi.53	0–415	738	65										3					1				×								1
		NORTHERN HOLIDAY EXPEDITION																															
2[18]	40° 23′	127° 04′ W.	1.viii.51	215	626	4	4		1														69		×	3	1	5				1	
3	40° 28′	129° 05′ W.	1.viii.51	210	789	6																											
4	40° 30′	131° 08′ W.	2.viii.51	183	832																												
5	30′ 22′	133° 06′ W.	3.viii.51	208	758	10						50											2			2							
6	40° 29′	134° 58′ W.	4.viii.51	213	739		2					9														1							
7[18]	40° 28′	137° 38′ W.	4.viii.51	213	728	14		2																		2		5					
8[16]	40° 21·5′	139° 24·5′ W.	5.viii.51	208	706	6						19													×	1							
9	40° 28′	141° 57′ W.	6.viii.51	196	723	7																											
11	40° 32′	145° 47′ W.	9.viii.51	203	745	1	1					8																					
12	40° 34′	147° 54·5′ W.	9.viii.51	226	699																					2							
13	30° 34′	149° 43′ W.	10.viii.51	215	721	6						20													×	1							
14	41° 41′	150° 00′ W.	11.viii.51	210	655	73						32									1				×	1	1						

TABLE 1—*contd.*

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³)	*Tomopteris elegans*	*Tomopteris septentrionalis*	*Tomopteris planktonis*	*Tomopteris ligulata*	*Tomopteris nisseni*	*Tomopteris apsteini*	*Tomopteris* not identifiable	*Naiades cantrainii*	*Vanadis formosa*	*Vanadis crystallina*	*Vanadis minuta*	*Vanadis longissima*	*Vanadis tagensis*	*Rhynchonerella gracilis*	*Rhynchonerella mobii*	*Rhynchonerella petersii*	*Rhynchonerella angelini*	*Plotohelmis tenuis*	*Krohnia lepidota*	*Alciopid* fragments	*Typhloscolex mulleri*	*Sagitella kowalewskii*	*Travisiopsis lobifera*	*Lopadorhynchus brevis*	*Lopadorhynchus uncinatus*	*Lopadorhynchus krohnii*	*Pelagobia longicirrata*	*Maupasia caeca*
15[18]	43° 8·5′	149° 50′ W.	11.viii.51	214	760	172						10														1							
16	44° 35′	150° 21′ W.	12.viii.51	191	921	5																				1							
17[16]	45° 58·5′	150° 11·5′ W.	13.viii.51	218	711	4																					1						
18	47° 25·5′	150° 4·5′ W.	13.viii.51	200	708																					2							
44	43° 14′	155° 55·5′ W.	8.ix.51	204	915	22						241																					
45	42° 15′	155° 36′ W.	9.ix.51	170	905	30						91									1					2							
46	41° 20′	155° 20′ W.	9.ix.51	212	811	6	36					109																					
47[16]	40° 09′	155° 03′ W.	10.ix.51	195	408	10						201										1			×								
48	39° 18′	154° 38′ W.	11.ix.51	211	700	1																											
49[18]	38° 30′	154° 25′ W.	11.ix.51	219	683	2						26										4			×								
50	37° 28′	154° 12′ W.	12.ix.51	217	754																1				×								
53	33° 30′	153° 05′ W.	14.ix.51	221	724	2		6					1		1	1					1				×		2				2		
54[17]	31° 58′	152° 25′ W.	15.ix.51	211	736	2		1	2			7	1			3				1	1		1		×	1	1						
55	30° 03′	152° 00′ W.	15.ix.51	208	772	5		22			1		1												×	1	1				1		
56	28° 06·5′	151° 25′ W.	16.ix.51	210	738	3		1	1		4	2			1	4									×	2	2		1		3	1	
57	29° 03′	149° 17′ W.	17.ix.51	215	793	1						7			1	1					1				×		3		1		1	1	
58	29° 45′	147° 05′ W.	18.ix.51	215	765	1		4				4				1				1				2	×	1	1						
59	30° 25′	145° 08′ W.	18.ix.51	220	714	3		1			2	4													×	2	2						
60	31° 19′	143° 02′ W.	19.ix.51	207	740	3		2	1				1	1	1	3				1					×		6		1		1		
61	32° 02′	140° 55′ W.	20.ix.51	198	768	3		2					1			3	1			1	1			1	×		2		5				
62	32° 46′	138° 50′ W.	20.ix.51	219	677	2		2								2			1					1	×	4	8				1		
63	33° 03′	136° 22·5′ W.	21.ix.51	206	803	7					4		1		1	5			1	2	1				×		9				1		
64	32° 53′	134° 13′ W	21.ix.51	197	756	5			1		3		1		2				1					1	×	4	3				1		
65	32° 52′	131° 58′ W	22.ix.51	181	817							15					1								×		6						
66[17]	32° 39′	129° 41′ W	23.ix.51	208	810	53										1									×		2				1		

TABLE I—*contd.*

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³)	*Tomopteris elegans*	*Tomopteris septentionalis*	*Tomopteris planktonis*	*Tomopteris ligulata*	*Tomopteris nisseni*	*Tomopteris apsteini*	*Tomopteris* not identifiable	*Naiades cantrainii*	*Vanadis formosa*	*Vanadis crystallina*	*Vanadis minuta*	*Vanadis longissima*	*Vanadis tagensis*	*Rhynchonerella gracilis*	*Rhynchonerella mobii*	*Rhynchonerella petersii*	*Rhynchonerella angelini*	*Plotohelmis tenuis*	*Krohnia lepidota*	Alciopid fragments	*Typhloscolex mülleri*	*Sagitella kowalewskii*	*Travisiopsis lobifera*	*Lopadorhynchus brevis*	*Lopadorhynchus uncinatus*	*Lopadorhynchus krohnii*	*Pelagobia longicirrata*	*Maupasia caeca*
		CHINOOK EXPEDITION																															
1	28° 42·3′	151° 47·2′ W.	8.vii.56	91	555	1		2				8			1									2	×	1	9			2	1		
2	32° 38′	154° 49·5′ W.	11.vii.56	130	472	1			1			10	1			1	1			2					×		8				2		
3	39° 56·3′	158° 38·5′ W.	15.vii.56	115	536							72									2				×			1					
4	42° 33′	162° 09′ W.	17.vii.56	100	498	10	6					42									1				×	13							
5	47° 01′	164° 55·5′ W.	19.vii.56	100	509																												
7	46° 28·3′	174° 29·3′ W.	31.vii.56	100	526		4					10														8		2					
8	40° 28′	173° 04′ W.	3.viii.56	100	523	1	2																			1	3	1			1		
9^{17}	32° 37·6′	172° 21·3′ W.	6.viii.56	94	573	2					4		1								1		1	1	×	14	5		1		4	2	
		P.O.F.I. *Hugh M. Smith* CRUISE No. 30																															
26	38° 48′	179° 52′ W.	28.vii.55	140	not known								1			1									×								
29	41° 50′	179° 54′ W.	29.vii.55	140	,,												1											1					
32	44° 56′	179° 49′ W.	30.vii.55	140	,,							19																1					
44	45° 05′	172° 30′ W.	4.viii.55	140	,,																												
46	43° 20′	172° 19′ W.	4.viii.55	140	,,							1										1					1						
70	37° 30′	164° 48′ W.	13.viii.55	140	,,							16	1																				
71	38° 59′	164° 50′ W.	14.viii.55	140	,,							4	2		1	1						4			×								
73	40° 28′	165° 00′ W.	14.viii.55	140	,,							17			1						1	1			×	1							
74	42° 03′	164° 52′ W.	15.viii.55	140	,,	1						40					2						1		×	1		1					
76	43° 29′	165° 02′ W.	15.viii.55	140	,,							11																					
77	44° 57′	165° 01′ W.	16.viii.55	140	,,																							1					
79	46° 29′	164° 56′ W.	16.viii.55	140	,,		49					67														1	1						
87	48° 04′	157° 24′ W.	20.viii.55	140	,,							8																					
89	46° 28′	157° 06′ W.	20.viii.55	140	,,							1														2	1	1					
90	44° 57′	157° 26′ W.	21.viii.55	140	,,		2					10														1							

TABLE I—*contd.*

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m^3)	*Tomopteris elegans*	*Tomopteris septentrionalis*	*Tomopteris planktonis*	*Tomopteris ligulata*	*Tomopteris nisseni*	*Tomopteris apsteini*	*Tomopteris* not identifiable	*Naiades cantrainii*	*Vanadis formosa*	*Vanadis crystallina*	*Vanadis minuta*	*Vanadis longissima*	*Vanadis tagensis*	*Rhynchonerella gracilis*	*Rhynchonerella mobii*	*Rhynchonerella petersii*	*Rhynchonerella angelini*	*Plotohelmis tenuis*	*Krohnia lepidota*	Alciopid fragments	*Typhloscolex mülleri*	*Sagitella kowalewskii*	*Travisiopsis lobifera*	*Lopadorhynchus brevis*	*Lopadorhynchus uncinatus*	*Lopadorhynchus krohnii*	*Pelagobia longicirrata*	*Maupasia caeca*
93	43° 23′	157° 24′ W.	21.viii.55	140	not known							62									1												
94	41° 56′	157° 22′ W.	22.viii.55	140	,,							171																					
96	40° 27′	157° 31′ W.	22.viii.55	140	,,	90											1				2				×							7	
97	38° 57′	157° 30′ W.	23.viii.55	140	,,							16																					
99	37° 26′	157° 30′ W.	23.viii.55	140	,,	5						4	1		2	1									×				1	1			
100	35° 56′	157° 30′ W.	24.viii.55	140	,,								1			2																	
102	34° 28′	157° 30′ W.	24.viii.55	140	,,	2			2				6		2	3					1				×		1						

[1] 1 *Pedinosoma curtum.*
[2] 1 *Travisiopsis levinseni.*
[3] Quarter of sample examined.
[4] 4 *Travisiopsis levinseni* : ¼ of the sample examined.
[5] 3 : 2 : 3 *Travisiopsis lanceolata* respectively.
[6] 1 : 2 : 2 *Tomopteris pacifica* respectively.
[7] Three-quarters of the sample examined.
[8] 1 *Travisiopsis lanceolata.*
[9] 1 : 6 : 1 : 1 : 3 *Travisiopsis dubia* respectively.
[10] 1 *Travisiopsis lanceolata.*
[11] 1 *Travisiopsis levinseni.*
[12] All 1 specimen of *Pedinosoma curtum* except 141A (2).
[13] 53 specimens of *Phalacrophorus uniformis.*
[14] 1 *Phalacrophorus pictus.*
[15] 1 *Pedinoson a curtum.*
At Northern Holiday Stn. 51, 36° 12·5 N., 153° 56 W., the net was torn, 1 specimen of *Naiades cantrainii* and some Alciopid fragments were present.
[16] Half of the sample examined.
[17] 1 *Travisiopsis lanceolagta.*
[18] 2 *Travisiopsis dubia.*

TABLE II.—*Species Collected at Stations in the Sub-Arctic Zone*

TRANS-PACIFIC EXPEDITION

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³.)	*Tomopteris septentrionalis*	*Tomopteris pacifica*	*Tomopteris* not identifiable	*Rhynchonerella angelini*	*Alciopid* fragments	*Typhloscolex mülleri*	*Pelagobia longicirrata*	*Phalacrophorus pictus*
19A	48° 14·2′	153° 20·1′ W.	6.viii.53	0–129	447	1		23			12		
B	"	"	"	164–282	332	9	10		1		16		
20A	49° 29·5′	154° 56·5′ W.	7.viii.53	0–153	451	1		31			37		
B	"	"	"	153–324	526	8	2	36			20		
21A	50° 25·0′	156° 37·0′ W.	8.viii.53	0–137	439	2		38			13		
B	"	"	"	0–115	1,277	3		156			30		
C	"	"	"	0–288	1,050	158	5	143			30	3	3
22A	51° 21·3′	158° 20·0′ W.	8.viii.53	0–129	479			8			7		
B	"	"	"	0–294	1,077	5		28			11		
23A	52° 10·4′	160° 08·0′ W.	9.viii.53	0–135	535	17		59			10		3
B	"	"	"	0–270	1,095	78	1	21			12		
24A	53° 15·0′	161° 55·0′ W.	9.viii.53	0–180	417			13					
B	"	"	"	135–270	351	7				×	27	2	4
C	"	"	"	288–637	462					×	7	34	3
25A	53° 32·5′	163° 20·8′ W.	10.viii.53	0–84	514	1		4					
B	"	"	"	137–318	351	55		4			4	12	1
C	"	"	"	270–594	464		1	7			3	4	1
D	"	"	"	525–1,175	1,860			11			2	105	
26A[1]	54° 00·0′	168° 19·8′ W.	13.viii.53	0–100	305	12					11		
27A	54° 00·0′	170° 03·0′ W.	13.viii.53	0–132	524			45			20		
B[1]	"	"	"	149–265	175	12					14		7
28A	53° 59·5′	171° 40·0′ W.	13.viii.53	0–145	433	18		5			4		1
B[2]	"	"	"	0–295	852	86	1				9		
29A[1]	54° 00·0′	173° 15·5′ W.	14.viii.53	0–180	262			10			3		
B[1]	"	"	"	165–360	166	5					8	1	9
C[1]	"	"	"	305–460	277					×	7	8	14
30A	53° 57·7′	175° 04·5′ W.	15.viii.53	0–125	433			1			5		
B[1]	"	"	"	0–300	472	3		10			6	1	
31A	53° 15·6′	175° 37·6′ W.	15.viii.53	0–105	439						10		
B	"	"	"	130–265	555	38		7			29		1
32A	52° 29·3′	176° 09·0′ W.	15.viii.53	0–105	543	2		20			7		8
B	"	"	"	115–265	370						4	1	
C	"	"	"	300–515	520						2	22	2
33A	52° 19·9′	176° 57·5′ W.	24.viii.53	0–125	478			4			3		2
B[2]	"	"	"	120–305	333		1				8		
34A	53° 10·3′	177° 59·0′ W.	25.viii.53	0–180	469	1		20			11		
B[2]	"	"	"	0–320	780	2					7		1
35A[3]	54° 05·5′	178° 56·2′ W.	25.viii.53	0–395	216	1	1	21			7		
36A	54° 00·9′	178° 58·7′ E.	26.viii.53	0–165	381	2					14		
B	"	"	"	0–290	787	30				×	77		
37A	53° 59·0′	176° 55·0′ E.	27.viii.53	0–140	400	14		30		×	67		
B	"	"	"	0–290	914	56		10		×	104		5

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[1] Half of the sample examined.
[2] Quarter of the sample examined.
[3] Eighth of the sample examined.

TABLE II.—*contd.*

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³.)	*Tomopteris septentrionalis*	*Tomopteris pacifica*	*Tomopteris* not identifiable	*Rhynchonerella angelini*	*Alciopid* fragments	*Typhloscolex mülleri*	*Pelagobia longicirrata*	*Phalacrophorus pictus*	*Maupasia caeca*
38A[2]	53° 59·1′	174° 49·0′ E.	28.viii.53	0–165	107	3								
B	,,	,,	,,	145–320	212	77	2				8		6	
39A	54° 03·1′	172° 28·8′ E.	30.viii.53	0–180	412			12			26			
B	,,	,,	,,	160–335	350	6	1				11	7	1	
40A	53° 57·0′	171° 10·8′ E.	30.viii.53	0–170	422	29					1			
B	,,	,,	,,	170–340	261		2				24	10		
C	,,	,,	,,	340–510	335						3	65		
D	,,	,,	,,	510–680	340							38		
E	,,	,,	30–31.viii.53	0–1,020	620	58	1	6			10	6		
41A	53° 32·1′	168° 50·8′ E.	31.viii.53	0–135	526	8					3			
B	,,	,,	,,	140–290	370	26	1				15	6		
42A	53° 32·4′	176° 10·8′ E.	1.ix.53	0–175	750	4					73			
B	,,	,,	,,	175–350	695	42			1		44			
C	,,	,,	,,	350–525	670	1					6	62		1
E	,,	,,	,,	0–1,050	587	21			1		15	45		
43A	53° 35·5′	173° 42·0′ E.	1.ix.53	0–155	402	4					14			
B	,,	,,	1–2.ix.53	0–325	1,043	10	1			×	20	5		
44A	53° 40·8′	161° 55·5′ E.	2.ix.53	0–170	482	20		28			13			
B	,,	,,	,,	155–335	351	20					30		4	
C	,,	,,	,,	320–565	462	2					7	46	1	
45A	52° 23·0′	163° 15·2′ E.	3.ix.53	0–35	277									
B	,,	,,	,,	0–105	498						6			
C	,,	,,	,,	40–145	259			1			20			
D	,,	,,	,,	150–300	425	54					36			
46A	51° 13·0′	164° 34·3′ E.	4.ix.53	0–170	1,010	19			1		8			
B	,,	,,	,,	170–340	740		4		1		30	2	2	
C	,,	,,	,,	340–510	720			4			16	52		
D	,,	,,	3–4.ix.53	0–1,015	4,165	25		5		×	6	4		
47A	49° 50·1′	165° 49·2′ E.	5.ix.53	0–20	267	2		20						
B	,,	,,	,,	0–155	567	15		53			6		1	
C	,,	,,	,,	35–150	166	2	1				2			
D	,,	,,	,,	160–275	499			1			15	11		
48A	48° 46·3′	166° 48·1′ E.	5.ix.53	0–25	163									
B	,,	,,	,,	0–100	500	19		21			35			
C	,,	,,	,,	35–115	278	5					36			
D[4]	,,	,,	,,	140–320	475	19					9	7		
49A	47° 35·7′	167° 44·8′ E.	6.ix.53	0–170	788	4		64			19			
B	,,	,,	,,	170–340	760	45	1				11		4	
C	,,	,,	,,	340–510	760						1	5		
D	,,	,,	,,	510–680	760							38		
E[5]	,,	,,	,,	0–1,015	359	1		65	1		6	12		
50A	46° 16·5′	168° 52·2′ E.	6.ix.53	0–145	478	16		19			10			
B[6]	,,	,,	,,	155–355	370	3	3	2	1		9	1		1
61A	45° 15·1′	158° 20·0′ E.	14.ix.53	0–129	527	15					18			
B[6]	,,	,,	,,	135–270	1,130	5		17	4	×	11			
C	,,	,,	,,	270–446	558		1	5	1		6	21		
62A	45° 57·8′	156° 52·5′ E.	14.ix.53	0–106	490	3		2			19			
B	,,	,,	,,	0–258	1,086	25					23			

[4] 1 *Rhynchonerella gracilis.*

[5] One tenth sample examined.

[6] 1 *Plotohelmis tenuis.* One *Sagitella kowalewskii* at Stn. 50B.

TABLE II.—*contd.*

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³.)	*Tomopteris septentrionalis*	*Tomopteris pacifica*	*Tomopteris* not identifiable	*Rhynchonerella angelini*	*Alciopid* fragments	*Typhloscolex mulleri*	*Pelagobia longicirrata*	*Phalacrophorus pictus*	*Maupasia caeca*
63A	46° 23·5′	155° 28·6′ E.	15.ix.53	0–129	545			3			4			
B	,,	,,	,,	135–270	408			5			27		1	
C	,,	,,	,,	270–374	685	25	1				30	9	1	
64A	46° 54·5′	153° 55·2′ E.	15.ix.53	0–157	436	18					36			
B	,,	,,	,,	75–318	444	19					23		1	
65A	45° 29·9′	154° 19·7′ E.	16.ix.53	0–124	500			2			3			
B	,,	,,	,,	147–340	1,166	4					37	1		
66A	44° 09·0′	152° 56·8′ E.	17.ix.53	0–168	529	12		20			67			
C	,,	,,	,,	276–506	814	1					1			
E	,,	,,	,,	0–1,020	3,810	4	2	109			15	10		
66A[1]	,,	,,	,,	0–700	300			210	1		17	36		
67A	43° 09·0′	151° 52·0′ E.	18.ix.53	0–97	583			9			8			
B	,,	,,	,,	0–176	1,118	14		4			20			
68A	42° 02·2′	150° 33·2′ E.	18.ix.53	0–103	490			42			8			
B	,,	,,	,,	132–276	407	28					32			
69A	40° 54·5′	149° 25·7′ E.	19.ix.53	0–141	465			24			1			
71A	40° 05·0′	146° 45·0′ E.	20.ix.53	0–28	276									
B	,,	,,	,,	0–132	445	2		7			5			
C	,,	,,	,,	135–270	444			35			17			1
72A	40° 25·3′	145° 29·3′ E.	20.ix.53	0–41	189			2						
B	,,	,,	,,	0–115	464	3		6			1			
C[8]	,,	,,	,,	153–270	370	16		24			21			
73A	40° 53·4′	143° 51·5′ E.	21.ix.53	0–40	352									
B	,,	,,	,,	0–141	435			8			1			
C	,,	,,	,,	173–390	1,128	1		1			18			
78A	37° 58·9′	146° 01·1′ E.	30.ix.53	0–141	473	3		13						
B	,,	,,	,,	160–330	370	1		13			2			

NORTHERN HOLIDAY EXPEDITION

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³.)	*Tomopteris septentrionalis*	*Tomopteris pacifica*	*Tomopteris* not identifiable	*Rhynchonerella angelini*	*Alciopid* fragments	*Typhloscolex mulleri*	*Pelagobia longicirrata*	*Phalacrophorus pictus*	*Maupasia caeca*
19	48° 48′	150° 00′ W.	14.viii.51	118	1,143	1					15			
21	51° 35′	149° 52′ W.	15.viii.51	222	669	2					7			
22a	52° 50′	149° 52′ W.	16.viii.51	205	715	10					9			
23	56° 28·5′	151° 39′ W.	29.viii.51	206	796	9					5			
24	55° 50′	151° 18′ W.	29.viii.51	200	847	8	1	20			5			
25	54° 52′	150° 53·5′ W.	30.viii.51	188	834	31					2			
26[7]	54° 08′	150° 23′ W.	30.viii.51	222	688	29		27	1		27			
27	53° 13′	149° 56′ W.	31.viii.51	182	759	22					1			
28	53° 13′	157° 36′ W.	31.viii.51	203	751	1					1			
29	53° 24·5′	153° 18′ W.	1.ix.51	227	693						5			
30	53° 34·5′	155° 00′ W.	1.ix.51	202	665	8					4			

[7] 1 *Rhynchonerella gracilis.*
[8] 1 *Travisiopsis lanceolata.*

Stn. No.	Latitude (N.)	Longitude	Date (local)	Depth (m.)	Volume water filtered (m³.)	*Tomopteris septentrionalis*	*Tomopteris pacifica*	*Tomopteris* not identifiable	*Rhynchonerella angelini*	*Alciopid* fragments	*Typhloscolex mulleri*	*Pelagobia longicirrata*	*Phalacrophorus pictus*	*Maupasia caeca*
31	54° 00′	156° 32′ W.	2.ix.51	219	668	21	1				7	1	1	
32	54° 18′	157° 58′ W.	2.ix.51	188	765	11					2			
36	51° 00′	158° 33′ W.	4.ix.51	182	887	37		10			3			
37	50° 01′	158° 16′ W.	5.ix.51	160	1,004	56		7			2			
38	49° 01′	157° 55′ W.	5.ix.51	189	788	32		4			37			
39	48° 06·5′	157° 27′ W.	6.ix.51	204	704	25					13			
40	47° 05·5′	157° 16′ W.	7.ix.51	214	703	10	1				4			
		CHINOOK EXPEDITION												
6	50° 21′	178° 36′ W.	29.vii.56	85	565	35					18			
		P.O.F.I. *Hugh M. Smith* CRUISE NO. 30												
37	49° 34′	179° 58′ W.	31.vii.55	145	Not known	46		8						
80	48° 07′	164° 55′ W.	17.viii.55	139	,,									
81	49° 29′	165° 00′ W.	17.viii.55	140	,,			4			4			
83	49° 42′	162° 25′ W.	18.viii.55	137	,,	1		16						
84	49° 48′	159° 40′ W.	19.viii.55	141	,,			12			3			
86	49° 35′	157° 22′ W.	19.viii.55	139	,,	1		18						

TABLE III.—*Collections of the University of Washington, Dept. of Oceanography*

Cruise BB—199—M.W.T.

	Position			Species collected
St.	N.	W.	Date	(and number of specimens)
20	48° 46·8′	129° 58·8′	2.vii.58	*Rhynchonerella angelini* (1).
30	49° 02·6′	133° 39·5′	4.vii.58	*Plotohelmis tenuis* (3).
34	49° 09·3′	134° 57·2′	4.vii.58	*Plotohelmis tenuis* (1).
55	49° 23·1′	140° 24·8′	7.vii.58	*Tomopteris septentrionalis* (1).
64	49° 36·9′	142° 45·9′	8.vii.58	*Tomopteris pacifica* (1).
75	49° 48·2′	145° 27·9′	9.vii.58	*Travisiopsis lobifera* (1).
80	49° 30·1′	145° 52·5′	9–10.vii.58	*Tomopteris pacifica* (1).
99	45° 41·5′	146° 25·4′	12.vii.58	*Tomopteris septentrionalis* (1).
110	43° 42·0′	146° 25·0′	13.vii.58	*Tomopteris elegans* (1).
115	42° 47·2′	145° 20·1′	14.vii.58	*Tomopteris elegans* (2).
128	40° 35·8′	142° 54·5′	15.vii.58	*Rhynchonerella angelini* (1).
136	39° 35·1′	141° 53·0′	16.vii.58	*Rhynchonerella angelini* (1).
137	38° 41·0′	141° 01·0′	16.vii.58	*Rhynchonerella angelini* (1).
138	38° 35·7′	140° 56·0′	16.vii.58	*Rhynchonerella angelini* (1).
140	38° 24·9′	139° 37·1′	17.vii.58	*Rhynchonerella angelini* (1).
144	38° 45·7′	138° 08·0′	17–18.vii.58	*Rhynchonerella angelini* (1).
150	39° 21·0′	136° 21·2′	18.vii.58	*Rhynchonerella angelini* (3).
151	39° 23·1′	136° 13·1′	18.vii.58	*Naiades cantrainii* (1).
153	39° 35·5′	135° 28·7′	18–19.vii.58	*Rhynchonerella angelini* (4).
157	39° 42·5′	135° 03·9′	19.vii.58	*Naiades cantrainii* (1).
158	39° 44·7′	134° 51·1′	19.vii.58	*Rhynchonerella angelini* (2).
159	39° 46·9′	134° 48·0′	19.vii.58	*Rhynchonerella angelini* (1).
160	40° 11·0′	133° 26·6′	19.vii.58	*Rhynchonerella angelini* (3).
161	40° 11·0′	133° 26·6′	19.vii.58	*Rhynchonerella angelini* (1).
167	40° 22′9′	131° 32·0′	20.vii.58	*Tomopteris elegans* (1).
171	39° 58·9′	130° 34·5′	21.vii.58	*Tomopteris elegans* (1).
172	39° 57·6′	130° 28·7′	21.vii.58	*Travisiopsis lobifera* (1).
173	39° 56·3′	130° 22·8′	21.vii.58	*Travisiopsis lobifera* (1).
174	39° 55·0′	130° 17·4′	21.vii.58	*Tomopteris elegans* (2).
179	38° 38·2′	125° 48·6′	23.vii.58	*Tomopteris septentrionalis* (1).
191	36° 40·0′	123° 21·0′	27.vii.58	*Travisiopsis lobifera* (1).
196	34° 49·0′	121° 03·5′	28.vii.58	*Tomopteris septentrionalis* (1).
228	33° 44·8′	125° 01·3′	3.viii.58	*Tomopteris elegans* (1).
235	33° 34·0′	126° 35·1′	4.viii.58	*Vanadis crystallina* (1).
241	32° 15·1′	128° 32·9′	4.viii.58	*Lopadorhynchus uncinatus* (1).
249	35° 02·5′	130° 08·8′	6–7.viii.58	*Tomopteris elegans* (1).
252	35° 10·1′	130° 11·9′	7.viii.58	*Tomopteris elegans* (2).
253	35° 13·1′	130° 12·7′	7.viii.58	*Rhynchonerella mobii* (1).
256	36° 44·3′	130° 51·0′	7–8.viii.58	*Lopadorhynchus uncinatus* (1). *Vanadis formosa* (1). *Rhynchonerella angelini* (1).
257	36° 47·9′	130° 52·9′	8.viii.58	*Naiades cantrainii* (1).
258	36° 51·8′	130° 54·3′	8.viii.58	*Naiades cantrainii* (1).
261	37° 03·4′	130° 58·5′	8.viii.58	*Rhynchonerella angelini* (1).
263	39° 19·8′	131° 48·6′	8–9.viii.58	*Rhynchonerella angelini* (1).

TABLE III.—*cont.*

St.	Position		Date	Species collected (and number of specimens)
	N.	W.		
264	39° 24·3′	131° 50·2′	9.viii.58	*Rhynchonerella angelini* (4). *Naiades cantrainii* (1).
266	39° 32·0′	131° 53·0′	9.viii.58	*Vanadis formosa* (1). *Vanadis longissima* (2).
268	39° 40·9′	131° 56·3′	9.viii.58	*Rhynchonerella angelini* (7).
275	41° 16·0′	133° 13·3′	10.viii.58	*Vanadis longissima* (1). *Rhynchonerella angelini* (2).
277	42° 41·8′	135° 17·0′	10–11.viii.58	*Rhynchonerella angelini* (1).
284	45° 10·5′	139° 27·2′	12.viii.58	*Tomopteris elegans* (1).

Cruise BB—202—MWT

St.	N.	W.	Date	Species collected (and number of specimens)
9	49° 52·8′	130° 30·0′	23.ix.58	*Travisiopsis lobifera* (1).
50	47° 52·1′	134° 28·2′	29.ix.58	*Tomopteris septentrionalis* (1).
71	47° 56·0′	128° 14·3′	1.x.58	*Tomopteris septentrionalis* (1).

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ADDENDA.

The International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology (1961) was published after this paper was in page proof and it has not therefore, been possible to incorporate the necessary alterations into the text but they are listed below—

For *Typhloscolex mülleri* read
  Typhloscolex muelleri—Articles 27 and 32 (c) (i).
For *Rhynchonerella petersii* read
  Rhynchonerella petersi—Article 31.
For *Lopadorhynchus krohnii* read
  Lopadorhynchus krohni—Article 31.

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